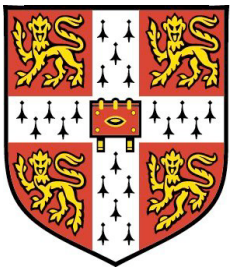
Comparative morphology and phylogeny of anomalodesmatan bivalves



André F. Sartori

Emmanuel College

University of Cambridge

This dissertation is submitted for the degree of

Doctor of Philosophy

2009

Declaration

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except where specifically indicated in the text.

The length of this dissertation does not exceed the maximum length specified by the Earth Sciences and Geography Degree Committee.

André F. Sartori

Acknowledgements

First and foremost, I would like to extend my sincere and particular thanks to Liz Harper for her unyielding encouragement, guidance and critical appraisal of this work. Without the generous gifts of a Gates Cambridge Scholarship, Overseas Research Students Award, Emmanuel College External Research Studentship, Cambridge Philosophical Society Research Studentship, Lundgren Research Award and travel grants from the Malacological Society of London and the Cambridge Philosophical Society, the research documented here would not have been possible. I am deeply grateful for these awards.

I am indebted to numerous colleagues who have helped in the acquisition of specimens, not only during field work, as gifts or loans, but also by providing curatorial assistance during visits to their institutions: Bruce Marshall (Museum of New Zealand Te Papa Tongarewa), Kathie Way, Amelia MacLellan, John Taylor and Emily Glover (The Natural History Museum), Luiz Simone, Osmar Domaneschi and Flávio Passos (Universidade de São Paulo), Kathe Jensen, Annie Vedelsby and Ole Tendal (Zoological Museum of the University of Copenhagen), Rüdiger Bieler and Jochen Gerber (Field Museum of Natural History), Lloyd Peck and Simon Morley (British Antarctic Survey), Juan da Rocha (Universidade de Santiago de Compostela), Alexandra Zieritz (University of Cambridge), Mathew Riley (Sedgwick Museum), José Tarasconi (Centro de Estudos Marinhos do Atlântico Sul), Paula Mikkelsen (American Museum of Natural History), Ian Loch (Australian Museum) and Brian Morton.

The specimens would have been fruitless without the training in scanning electron microscopy and preparation of shell sections kindly provided in the Department of Earth Sciences by Ian Marshall and Keith Gray, respectively. Histological sections were prepared in the Multi-imaging Centre of the University of Cambridge, with assistance from Lyn Carter. I benefitted from

the expertise of Alexander Ball whilst carrying out confocal microscopy in the Natural History Museum (London). The program TNT, which I used for parsimony analyses, was made available with the sponsorship of the Willi Hennig Society.

I acknowledge the staff of the Department of Earth Sciences for support over the course of my studies, in particular Sarah Humbert, Clare Pryke and Libby Tilley for their help and patience during countless literature searches.

The critical comments of Robert Prezant, Brian Morton and Nikolaus Malchus on portions of the chapters dealing with arenophilic glands and ligament structure contributed to their improvement. I also thank Darío Lazo for his comments of on the taxonomy of early Cretaceous *Pholadomya* and Alberto Villari for commenting on the hinge architecture of *Clavagella aperta*. These colleagues are, of course, exempt from any inaccuracies contained or implied by the contents of this volume.

For their continuing support of my endeavours abroad, I offer heartfelt thanks to my friends and family in Brazil. I also want to thank my friends and colleagues in Emmanuel College, Gates Cambridge Society and in the Department of Earth Sciences, who have made my time in Cambridge both enjoyable and memorable.

Last but certainly not least, I thank Paraminder for her love, support and all the good times over these years.

Comparative morphology and phylogeny of anomalodesmatan bivalves

by André F. Sartori

Anomalodesmatans comprise a large, ancient and ecologically diverse group of marine bivalves, but are nonetheless inconspicuous in most extant shallow water communities. For various reasons, which include their present scarcity and a bewildering array of disparate morphologies, representatives of the group have always proved difficult to interpret, and their systematics lagged behind those of most other major bivalve taxa.

Most of this dissertation reports the results of a comparative investigation on the shell morphology and anatomy of extant anomalodesmatans, which formed the basis for a reassessment of hypotheses of primary homology established by previous investigators and identification of novel characters for phylogenetic inference.

Due to the chief role played by the hinge ligament in authoritative discussions of anomalodesmatan evolution, this organ was chosen as the focus of a more detailed treatment. Discontinuous ontogeny of fibrous ligament is shown to characterise several members of the group, with the implication that, in contrast to the prevailing model, not all anomalodesmatan adult ligaments may be considered homologous.

Likewise, a system of multicellular glands concerned with sediment agglutination was studied with particular emphasis because it is both exclusive to and widespread within Anomalodesmata. Evidence of preserved glandular secretion is recorded for the first time in fossil material and the glands themselves found in extant laternulids and pholadomyids, thus considerably expanding their known taxonomic distribution.

Finally, this volume also documents the largest cladistic analysis of extant anomalodesmatans performed to date, including morphological data compiled from both original observations and literature accounts. Among traditionally recognised superfamilies, Pholadomyoidea, Clavagelloidea and Septibranchia were found monophyletic. Taxa commonly referred to Pandoroidea and Thracioidea were recovered as part of two new clades, which are also supported by recent molecular studies.

Interpreted in the light of the fossil record, reconstructed phylogenetic relationships favour the iterative evolution of shallow infaunal and epifaunal anomalodesmatans from deep-burrowing ancestors over previously advanced patterns for the history of the clade, namely ventral migration of the ligament and irreversible radiations into a deep infaunal life habit.

Contents

1 Introduction and current state of anomalodesmatan systematics 1

1.1 Anomalodesmatan taxa . . . 2

1.1.1 Pholadomyoidea . . . 2

1.1.2 Thracioidea . . . 4

1.1.3 Pandoroidea . . . 5

1.1.4 Clavagelloidea . . . 7

1.1.5 Septibranchia . . . 7

1.2 Search for phylogenetic relationships . . . 10

1.2.1 Sister group relationships and monophyly of Anomalodesmata . . . 12

1.2.2 Relationships within the Anomalodesmata . . . 14

1.3 Aims and outline of the present study . . . 17

2 Structure and development of the anomalodesmatan ligament 19

2.1 Definitions . . . 20

2.2 Material and Methods . . . 21

2.2.1 Detailed study of *T. phaseolina* . . . 21

2.2.1.1 Measurements and Allometric Analysis . . . 21

2.2.1.2 Functional analysis . . . 23

2.2.1.3 Confocal Microscopy . . . 23

2.2.1.4 Scanning Electron Microscopy (SEM) . . . 24

2.2.2 Comparative study of other anomalodesmatans . . . 25

2.3 Post-larval development of the ligament of *T. phaseolina* . . . 25

2.3.1 Observations . . . 25

2.3.1.1 Internal Ligament . . . 25

2.3.1.2 Parivincular Ligament . . . 29

2.3.1.3 Allometry . . . 29

2.3.2 Previous Models of Ligament Structure in *Thracia* 33
2.3.3 Discontinuous Ligament Ontogeny 35
2.3.4 Functional Morphology of F1 and Associated Lithodesma 36
2.4 Comparative morphology of the ligament in extant anomalodesmatans . 36
2.4.1 Thracioidea 37
2.4.2 Pholadomyoidea 45
2.4.3 Clavagelloidea 48
2.4.4 Pandoroidea and Septibranchia 52
2.5 A new model for the evolution of anomalodesmatan ligament systems . 55

3 Form, function and evolution of the arenophilic glandular system 62
3.1 Material and methods 64
3.1.1 Extant material 64
3.1.1.1 Observations *in vivo* 64
3.1.1.2 Observations of dried shells and preserved soft parts . . 64
3.1.2 Fossil material 65
3.2 Arenophilic system in extant forms 65
3.2.1 Laternulidae 65
3.2.2 Pholadomyidae 70
3.2.3 Comparative anatomy 73
3.2.3.1 Corporeal distribution 73
3.2.3.2 Histology and cytology 76
3.2.3.3 Topology and pallial origin 77
3.2.4 Recognition of arenophilic secretion 80
3.3 Arenophilic system in fossil taxa 81
3.3.1 Records of fossilised arenophilic lines 81
3.3.2 Mode of preservation 84
3.4 Phylogenetic considerations 84

4 A reappraisal of anomalodesmatan morphological characters 90
4.1 Material and methods 91
4.2 Conchological characters 92
4.2.1 Shell microstructure 92
4.2.1.1 Previously described anomalodesmatan microstructural types 92
4.2.1.2 Plesiomorphic arrangement 93

4.2.1.3 Anomalodesmatan “homogeneous” microstructures . . 94
4.2.1.4 Novel microstructural arrangements 96
4.2.2 Calcified periostracal sculpture 97
4.2.2.1 Homology of the elements 97
4.2.2.2 Diversity of form and distribution on the shell wall . . . 99
4.2.3 Hinge teeth 100
4.2.4 Umbonal slit 102
4.2.5 Crypt 104
4.2.6 Cementation 105
4.3 Mantle and siphons 105
4.3.1 Mantle fusion and fourth pallial aperture 105
4.3.2 Pigmentation 107
4.3.3 Pallial glands 108
4.3.4 Pallial muscles 108
4.3.5 Siphonal retractors 108
4.3.6 Histology of the siphonal walls 110
4.3.7 Mucus-lined siphonal passages 110
4.3.8 Tentacles and sense organs 110
4.3.9 Siphonal cowl 112
4.4 Gills and labial palps 112
4.4.1 Nature and alignment of the gills 112
4.4.2 Arrangement and morphology of the filaments 115
4.4.3 Ctenidial unions 115
4.4.4 Morphology of the labial palps 117
4.4.5 Marginal food groove and association of gills to labial palps . . . 117
4.5 Foot and statocysts 118
4.5.1 Byssal apparatus in adults 118
4.5.2 Opisthopodium 118
4.5.3 Pedal retractors 118
4.5.4 Statocysts 119
4.6 Digestive tract 120
4.6.1 Oesophagus 120
4.6.2 Stomach 121
4.6.3 Path of the intestine 124
4.7 Reproduction 124

5 Cladistic analysis **126**

5.1 Material and methods . . . 127
5.1.1 Taxonomic sampling . . . 127
5.1.2 Character analysis and coding . . . 130
5.1.3 Phylogenetic analyses . . . 132
5.1.3.1 Character state reconstructions . . . 133
5.2 Results . . . 133
5.2.1 Scope . . . 133
5.2.2 Analyses of the complete dataset . . . 134
5.2.3 Analyses with restricted taxa . . . 137
5.2.4 Clades and apomorphies . . . 138
5.2.4.1 Clade A: Anomalodesmata . . . 138
5.2.4.2 Clade B: Pandoridae . . . 139
5.2.4.3 Clade C . . . 141
5.2.4.4 Clade D: Pholadomyoidea . . . 141
5.2.4.5 Clade E . . . 142
5.2.4.6 Clade F: Lyonsiidae + Laternulidae + Clavagelloidea . 142
5.2.4.7 Clade G: Clavagelloidea . . . 143
5.2.4.8 Clade H: Lyonsiidae + Laternulidae . . . 143
5.2.4.9 Clade I . . . 144
5.2.4.10 Clade J: Septibranchia . . . 144
5.2.4.11 Clade K: Thraciidae + Periplomatidae + Myochamidae + Cleidothaeridae . . . 146
5.2.4.12 Clade L: Periplomatidae . . . 147
5.2.4.13 Clade M: Cleidothaeridae . . . 148
5.2.4.14 Clade N: Thraciidae (part) + Myochamidae (part) . . . 149
5.3 Discussion . . . 150
5.3.1 Character fit . . . 150
5.3.2 Suggested relationships . . . 150
5.3.2.1 *Thracidora arenosa* and Spheniopsidae . . . 150
5.3.2.2 Pandoridae . . . 151
5.3.2.3 Pholadomyoidea . . . 152
5.3.2.4 Pandoroidea sensu Newell *et al.* . . . 153
5.3.2.5 Pandoroidea and Thracioidea sensu Boss . . . 155
5.3.2.6 Periplomatidae . . . 157

5.3.2.7 Septibranchia 159
5.4 Conclusions 160

6 Anomalodesmatan phylogeny and evolutionary trends 161
6.1 Fossil record 162
6.1.1 Ucumariidae and other Early Ordovician taxa 162
6.1.2 Modiomorphoidea 164
6.1.3 Orthonotoida 166
6.1.4 Edmondioidea 167
6.1.5 Ceratomyoidea 168
6.1.6 Pholadomyoidea 169
6.1.7 Extant families 171
6.2 Tentative phylogeny of extant anomalodesmatans 172
6.3 Evolutionary trends 174
6.3.1 Ventral migration of the ligament 174
6.3.2 Adaptations for deep-burrowing 174
6.3.3 Heterochronic evolution 175
6.3.3.1 Clavagelloids, pandorids and lyonsiids as offshoots of Laternulidae 175
6.3.3.2 Cleidothaerids and myochamids as offshoots of Thraciidae 176
6.3.3.3 Processes 176

Conclusions 178

References 181

A List of examined extant material 206

B Simple and full allometric equations 212

C Character definitions 217

List of Figures

1.1 Shell morphology and gross anatomy of extant pholadomyoids 3
1.2 Shell morphology and gross anatomy of extant thracioids 5
1.3 Shell morphology and gross anatomy of extant pandoroids 6
1.4 Crypt morphology and gross anatomy of extant clavagelloids 8
1.5 Shell morphology and gross anatomy of extant septibranchs 9
1.6 Current understanding of bivalve phylogenetic relationships 13
1.7 Cladistic hypotheses of anomalodesmatan interrelationships 16

2.1 Hinge of *Thracia phaseolina* and placement of measurements 22
2.2 Ligament morphology in a growth series of *Thracia phaseolina* 26
2.3 Ligament attachment areas and ultrastructure of the lithodesma of *Thracia phaseolina* 27
2.4 Confocal images of the ligament of *Thracia phaseolina* 28
2.5 Allometry of the ligament components of *Thracia phaseolina* 32
2.6 Lithodesma morphology in a growth series of *Thracia phaseolina* 34
2.7 Diversity of ligament morphologies in adult thracioids 38
2.8 Morphological aspects of the ligament of *Thracia meridionalis* 40
2.9 Ligament morphology in *Periploma compressum*, *Laternula truncata* and *Trigonothracia jinxingae* 41
2.10 Morphological aspects of the ligament of *Laternula elliptica* 43
2.11 Morphological aspects of the ligament of *Thracia similis* 44
2.12 Ligament morphology in *Parvithracia fragilissima* and *Asthenothaerus maxwelli* 44
2.13 Morphological aspects of the ligament of pholadomyoids 47
2.14 Morphological aspects of the ligament of clavagelloids 51
2.15 Ligament morphology in selected pandoroid and septibranch taxa 53
2.16 Hypothesized transitions between anomalodesmatan ligament grades . 60

3.1 Left view of *Laternula truncata* 66
3.2 Arenophilic secretion on the siphons of *Laternula* 67
3.3 Lateral view of the siphons of *Laternula elliptica* 68
3.4 Transverse sections through the siphons of *Laternula* 68
3.5 Histology of arenophilic glands in *Laternula* 69
3.6 Juvenile arenophilic gland and encrustations on *Laternula* 71
3.7 Arenophilic systems of *Pholadomya candida* and *Lyonsia* 72
3.8 Topology and histology of the arenophilic glands of *Pholadomya candida* 73
3.9 Topology of the arenophilic glands of *Lyonsia norwegica* 77
3.10 Morphology and histology of arenophilic papillae in *Lyonsia norwegica* . 79
3.11 Fossilised arenophilic secretion in *Pholadomya* and *Pleuromya* 83
3.12 Reconstructions of character states transitions for absence/presence of an arenophilic system 86

4.1 Relationship between mantle and shell of *Anodonta cygnea* 93
4.2 Shell microstructure in *Cardiomya cleryana* and selected thraciids . . . 94
4.3 Shell microstructure of selected anomalodesmatans 96
4.4 Calcified periostracal elements 99
4.5 Hinge teeth, umbonal slit and crypt morphology 102
4.6 Organs of the pallial cavity of *Periploma compressum* 107
4.7 Anatomical and histological aspects of the anomalodesmatan mantle . . 109
4.8 Pallial musculature 111
4.9 Tentacles, sense organs and other structures associated with anomalodesmatan siphons 113
4.10 Organs of the pallial cavity of *Cardiomya cleryana* 114
4.11 Histological aspects of anomalodesmatan ctenidia 116
4.12 Characters associated with the intersiphonal septum, foot, statocysts and oesophagus of anomalodesmatans 119
4.13 Pedal musculature and digestive tract of *Periploma compressum* 121
4.14 Pedal musculature and digestive tract of *Cardiomya cleryana* 122

5.1 Strict consensus trees recovered in analyses of the complete dataset . . . 135
5.2 Majority-rule consensus cladograms produced by analyses of the complete dataset 136
5.3 Strict consensus tree produced by analyses of the reduced dataset 138

5.4 Character optimisation on the strict consensus tree produced by analysis of the reduced dataset 140

6.1 Generic diversity in each anomalodesmatan family over the course of the Phanerozoic 163
6.2 Major extinct anomalodesmatan groups 165
6.3 Phylogeny of extant anomalodesmatans 173

List of Tables

2.1 Measurements taken from specimens of *Thracia phaseolina* 30
2.2 Summary statistics for allometric plots of the ligament components of *Thracia phaseolina* 33

3.1 Diameter of the arenophilic glands of selected laternulids 70
3.2 Specimens displaying fossilised arenophilic secretion 82
3.3 Taxonomic distribution of arenophilic glands 87

5.1 Data sources for terminals included in cladistic analyses 127
5.2 Data matrix subjected to cladistic analyses 131
5.3 Taxon prunings which improved resolution of the strict consensus trees produced by analyses of the complete matrix 137

Chapter 1

Introduction and current state of anomalodesmatan systematics

The Anomalodesmata is an exclusively marine, cosmopolitan group of bivalved molluscs, which comprises some one hundred extant genera and subgenera distributed from the intertidal zone to hadal depths (Harper *et al.*, 2006, table 1).

Modern anomalodesmatans display a remarkable variety of life habits, including shallow and deep-burrowing, nestling in crevices, and attachment to hard substrata by either byssal threads or cementation. The group also includes the bizarre watering-pot shells (Clavagelloidea), which live concealed in a tubular crypt and may occur either burrowed in soft sediments or boring into rocks or corals (Savazzi, 1999; Harper & Morton, 2004; Morton, 2007). In terms of feeding habits, most anomalodesmatans are suspension feeders and detritivores, but in deeper waters the group includes numerous genera of scavengers and predators that are capable of ingesting items ranging from forams to small gastropods and arthropods (Reid & Reid, 1974; Krylova, 2001).

The various adaptations that attend such a wide diversity of ecologies has led to drastic morphological changes in their body plan, turning Anomalodesmata into one of the most heterogeneous bivalve clades. This appears to have been a relatively recent phenomenon because prior to the Cenozoic the group was represented solely by burrowers and byssate forms (Bambach, 1971; Runnegar, 1974; Fang & Morris, 1997). A curious aspect of this extraordinary adaptive radiation is that it seems to have occurred concomitant with a loss of abundance in typical shallow water environments. Whereas Palaeozoic and Mesozoic anomalodesmatans were rather common (Runnegar, 1966; Bambach, 1971), most extant species figure among the least conspicuous elements of their communities, particularly at low latitudes (e.g. Frith *et al.*, 1976; Denadai *et al.*,

2001; Lourido *et al.*, 2006; Krug *et al.*, 2007). As Runnegar (1974, p. 904) notes, the clade "contains the rarest living bivalves—those without common names, usually found only in deep water or remote parts of the world, and rarely seen even by professional malacologists".

Predictably, the combination of bewildering morphological diversity with methodological difficulties arising from their present scarcity means that Anomalodesmata has remained one of the least understood bivalve higher taxa. The clade is diagnosed by a collection of conchological and anatomical characters that were last reviewed by Morton (1985*a*). These include a prismato-nacreous shell ornamented by granules or spicules, calcified ossicle associated with the ligament, fourth pallial aperture, hermaphroditism, lecithotrophic development and pallial glands responsible for agglutinating sediment particles. However, because none of these features is present in all anomalodesmatans and most occur in several other bivalve groups, there has been considerable scope for the proliferation of conflicting classificatory systems, differing widely in composition and arrangement. In the *Treatise on Invertebrate Paleontology*, which set the basis for later reviews, 12 extant anomalodesmatan families distributed in four superfamilies and a single order were recognised, although Newell (in Newell *et al.*, 1969*b*, p. N213) regarded the group as "probably artificial". Subsequent workers refined that classificatory scheme, suggesting the inclusion of additional taxa in the clade, altering taxonomic ranks and subdividing several of the component families.

The objective of this introductory chapter is to provide a concise overview of extant anomalodesmatan taxa, and review previous ideas regarding their phylogenetic relationships. These will furnish the necessary background for the analytical chapters that follow.

1.1 Anomalodesmatan taxa

1.1.1 Pholadomyoidea

Despite being the largest anomalodesmatan superfamily in terms of generic and suprageneric diversity and, ranging from Ordovician to Recent, also the one with the longest stratigraphic distribution (Morris *et al.*, 1991), Pholadomyoidea is represented today by few, rare species (probably less than 20) with restricted geographic distributions (Morton, 1982).

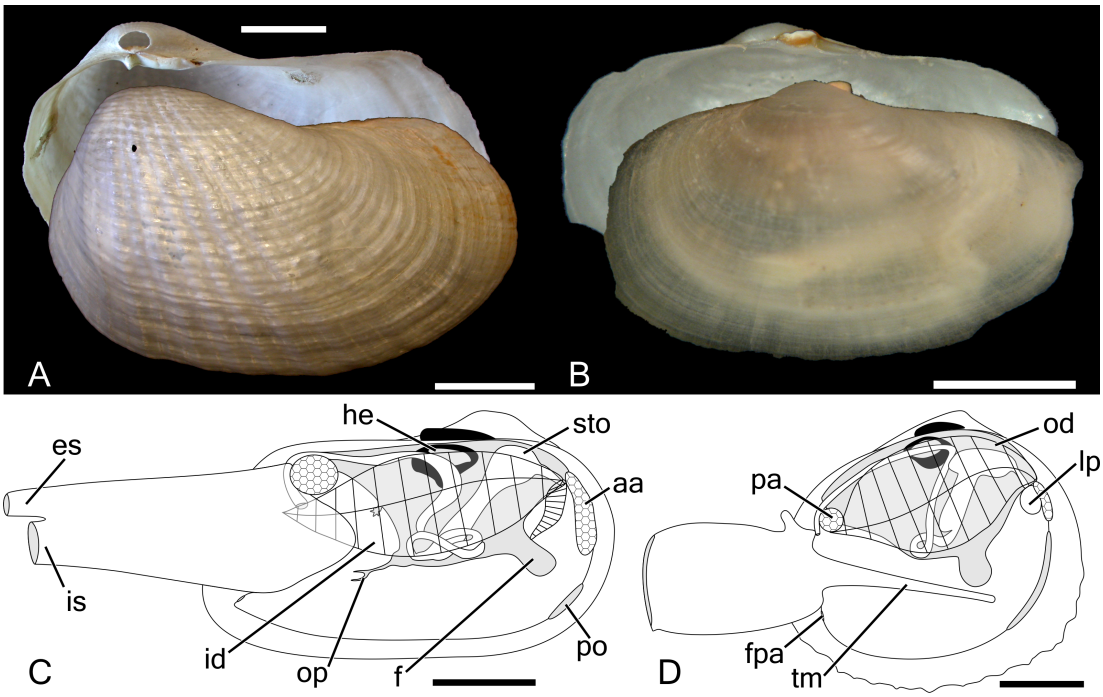


Figure 1.1: Shell morphology and gross anatomy of extant pholadomyoids. **A** and **B**. Left view of the shells of *Pholadomya candida* (unmatched valves; ZMUC, unregistered, St Thomas, leg. H. Bang) and *Parilimya neozelanica* (NMNZ M. 183055. 2004030), respectively. **C** and **D**. Schematic drawings of the gross anatomy of *P. candida* (after Morton, 1980) and *Parilimya fragilis* (after Morton, 1982), respectively, viewed from the right side. Abbreviations: **aa**, anterior adductor muscle; **es**, exhalant siphon; **f**, foot; **fpa**, fourth pallial aperture; **he**, heart; **id**, inner demibranch; **is**, inhalant siphon; **lp**, labial palp; **od**, outer demibranch; **op**, opisthopodium; **pa**, posterior adductor muscle; **po**, pedal opening; **sto**, stomach; **tm**, taenioid muscle. Scale bars: **A** and **C** = 2 cm; **B** and **D** = 5 mm.

Extant pholadomyoids are deep-burrowers with prismato-nacreous shell microstructure, permanent gapes, granular ornamentation, external parivincular ligament and often bearing radial ridges covering only part of the shell flank (Fig. 1.1). Except for brief comments on the life position and habitat of an individual of *Pholadomya candida* recently collected alive in Colombia (Diaz *et al.*, 2009), nothing is known of the behaviour and physiology of pholadomyoids, and most current knowledge of their anatomy comes from studies of preserved specimens of *P. candida* (Owen, 1842, 1845, 1855; Runnegar, 1972; Morton, 1980) and *Parilimya* species (Soot-Ryen, 1966; Morton, 1982; Krylova, 2006).

Recognition of striking anatomical differences between these two genera resulted in the allocation of *Parilimya* and related forms (*Panacca* and *Nipponopanacca*) to a separate family, Parilimyidae, leaving only *Pholadomya* in Pholadomyidae (Morton,

1982). Among other features, *Parilimya* differ from *Pholadomya* in the possession of specialised siphonal retractors with a separate area of insertion on the shell wall (taenioid muscles), small labial palps and a saccular stomach (Fig. 1.1). Morton (1982) interpreted these attributes as evidence of a carnivorous diet in parilimyids, but there is no direct evidence from stomach contents of dissected specimens.

1.1.2 Thracioidea

This is a heterogeneous assemblage comprising three families of deep and moderately deep burrowers which share a calcified ossicle placed immediately anterior to the main portion of the ligament.

Thraciids and periplomatids are cosmopolitan and have been recovered from intertidal to abyssal depths (Allen, 1958, 2008; Pelseneer, 1911). The siphons in these two families are fully separated (Fig. 1.2) and observations *in vivo* have shown that at least some species build mucous lined tubes, allowing them to burrow deeper than the maximum extent of their protruded siphons (Yonge, 1937; Morton, 1981*a*; Sartori & Domaneschi, 2005).

The family Laternulidae comprises a number of uncommon or only locally abundant species typically found on sand and mud flats throughout the Indo-Pacific (Morton, 1976; Prezant *et al.*, 2008), as well as one species, *Laternula elliptica*, which is well-represented in Antarctic and sub-Antarctic waters. Additionally, following the opening of the Suez canal, the type species of the family, *L. anatina*, has been successively recorded in the east border of the Mediterranean Sea (Barash & Danin, 1972). *L. elliptica* is one of the largest and most abundant Antarctic bivalves (Nicol, 1966; Dell, 1990) and for these reasons has become a model organism for Antarctic research, being without doubt the most studied anomalodesmatan (e.g. Urban & Mercuri, 1998; Mercuri *et al.*, 1998; Dick *et al.*, 2007; Peck *et al.*, 2007; Sato-Okoshi & Okoshi, 2008).

Laternulids share with periplomatids a similar hinge structure (Allen, 1960*a*; Morton, 1976, 1981*a*; Savazzi, 1990), both displaying an internal ligament held by spoon-shaped processes (chondrophores), which are reinforced by longitudinal ridges connected to the shell wall (butresses or clavicles). Additionally, a slit through the shell walls, normally sealed by periostracum, runs on each valve from the beak toward the ventral margin in both families, at times extending for as much as a third of the shell height (umbonal slit or crack).

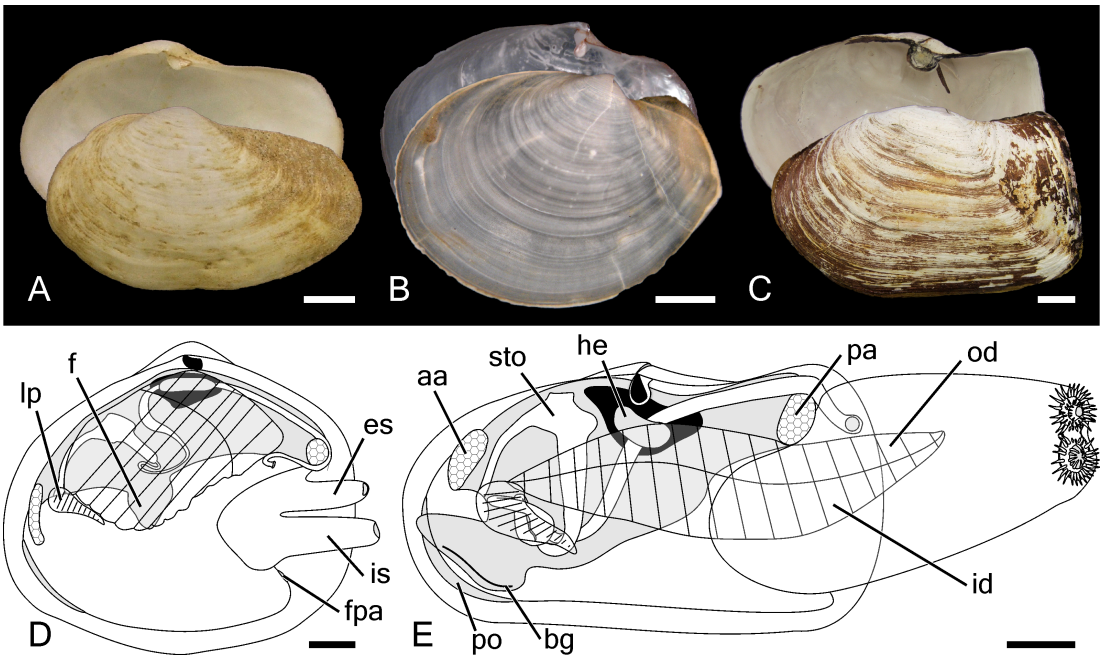


Figure 1.2: Shell morphology and gross anatomy of extant thracioids. **A**–**C**. Left view of the shell of the thraciid *Thracia similis* (MZSP 19.972), periplomatid *Periploma compressum* (CENEMAR, unregistered; Bombinhas, SC, Brazil) and laternulid *Laternula elliptica* (Hangar Cove), respectively. **C** and **D**. Schematic drawings of the gross anatomy of the thraciid *Parvithracia fragilissima* (NMNZ M. 155144) and laternulid *L. elliptica* (Admiralty Bay), respectively. Abbreviations: **aa**, anterior adductor muscle; **bg**, byssal groove; **es**, exhalant siphon; **f**, foot; **fpa**, fourth pallial aperture; **he**, heart; **id**, inner demibranch; **is**, inhalant siphon; **lp**, labial palp; **od**, outer demibranch; **pa**, posterior adductor muscle; **po**, pedal opening; **sto**, stomach. Scale bars: **A** = 5 mm; **B** = 3 mm; **C** = 10 mm; **D** = 1 mm; **E** = 10 mm.

1.1.3 Pandoroidea

Pandoroidea is the most diverse anomalodesmatan superfamily in terms of life habits. The superfamily includes shallow burrowers (Pandoridae, Lyonsiidae and Myochamidae, see Allen & Allen, 1955; Morton, 1977), endo and epi-byssate species (Lyonsiidae, see Ansell, 1967; Prezant, 1981*a*), cemented forms (Cleidothaeridae and Myochamidae, see Morton, 1974; Harper & Morton, 2000) and *Mytilimeria nuttalli*, a lyonsiid which lives in association with tunicates (Yonge, 1952).

The unifying morphological features of this ecological diverse assemblage are an internal ligament supported by a central calcified ossicle and filter-feeding gills (Boss, 1978; Yonge & Morton, 1980). Representatives of all pandoroid families are markedly inequivalve, except for some lyonsiids that are only moderately so (Fig. 1.3).

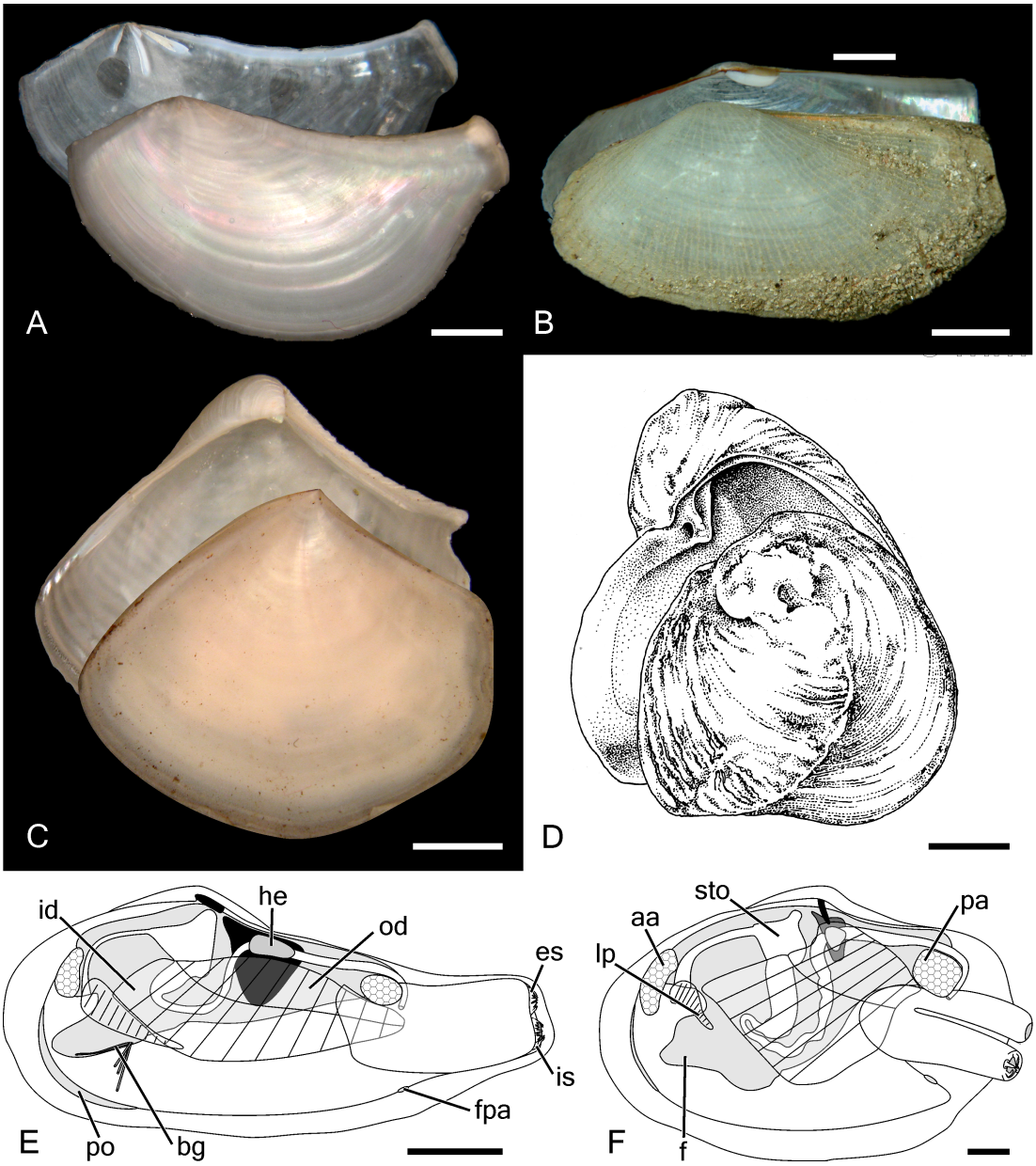


Figure 1.3: Shell morphology and gross anatomy of extant pandoroids. **A**–**D**. Left view of the shell of the pandorid *Frenamya elongatus* (Moreton Bay), lyonsiid *Lyonsia norwegica* (unmatched valves. Left valve: BMNH 1911.10.26.50090-50109; right valve: BMNH 20070070), myochamid *Myadora brevis* (Moreton Bay) and cleidothaerid *Cleidothaerus albidus* (after Prezant (1998*a*)), respectively. **E** and **F**. Schematic drawings of the gross anatomy of the lyonsiid *Lyonsia floridana* (BMNH 20070071) and myochamid *Hunkydora novozelandica* (NMNZ M. 183056. 2004030), respectively. Abbreviations: **aa**, anterior adductor muscle; **bg**, byssal groove; **es**, exhalant siphon; **f**, foot; **fpa**, fourth pallial aperture; **he**, heart; **id**, inner demibranch; **is**, inhalant siphon; **lp**, labial palp; **od**, outer demibranch; **pa**, posterior adductor muscle; **po**, pedal opening; **sto**, stomach. Scale bars: **A** to **C** = 3 mm; **D** = 10 mm; **E** and **F** = 2 mm.

Regarding their geographic distribution, extant pandorids and lyonsiids are cosmopolitan but apparently most abundant and diverse in the northern hemisphere, whereas myochamids and cleidothaerids are restricted to shallow waters in Australasia.

1.1.4 Clavagelloidea

Clavagelloids are readily distinguished from all other anomalodesmatans by their cryptic habit and unusual morphology, which has often been described as bizarre (Fig. 1.4). Pojeta & Sohl (1987), for example, regarded a Cretaceous member of the group as "the ultimate variation on the bivalve paradigm", while Smith (1998, p. 413) considered Clavagellidae "the most aberrant of the bivalve families with respect to shell form and life style". The taxon includes nestlers, borers, cemmenting and endobenthic species and has been the subject of numerous recent publications, including detailed accounts of the conchology and anatomy of particular extant species (e.g. Harper & Morton, 2004; Morton, 2002*a*,*b*, 2003*a*, 2004*a*,*b*,*c*, 2005, 2006*a*,*b*), as well as biogeographical and systematic treatments (e.g. Smith, 1971, 1976; Pojeta & Sohl, 1987; Savazzi, 1999, 2000, 2005; Morton, 2007).

Savazzi (1999, 2005) suggested Clavagelloidea might comprise two distinct lineages, which Morton (2007) ranked as families. Representatives of the first (Clavagellidae) have an internal ligament (without lithodesma) supported by chondrophores, both adductor muscles, a pallial sinus and the right valve free from the walls of the crypt or tube. Conversely, Morton (2007) notes that the second lineage (Penicillidae) exhibits an external ligament with lithodesma, both valves incorporated to the wall of a tubular crypt, the latter with anterior tubules extending from its anterior end (water pot), and lacks both a pallial sinus and adductor muscles as adults.

Extant clavagelloids are most diverse in clear, shallow waters of the Indo-Pacific and Australasian regions, with only a few species occurring in the Red Sea and Mediterranean (Smith, 1962*a*). Their known fossil record indicates that by the end of the Cretaceous the group maintained a marginal Tethyan distribution, occurring in both North America and the Old World (Jones & Nicol, 1989), but subsequently expanded eastward while becoming extinct in the western hemisphere (Smith, 1962*a*).

1.1.5 Septibranchia

Septibranchia comprises small (typically less than 1 cm in length), macrophagous anomalodesmatans with raptorial siphons, saccular stomach and either a pumping muscular

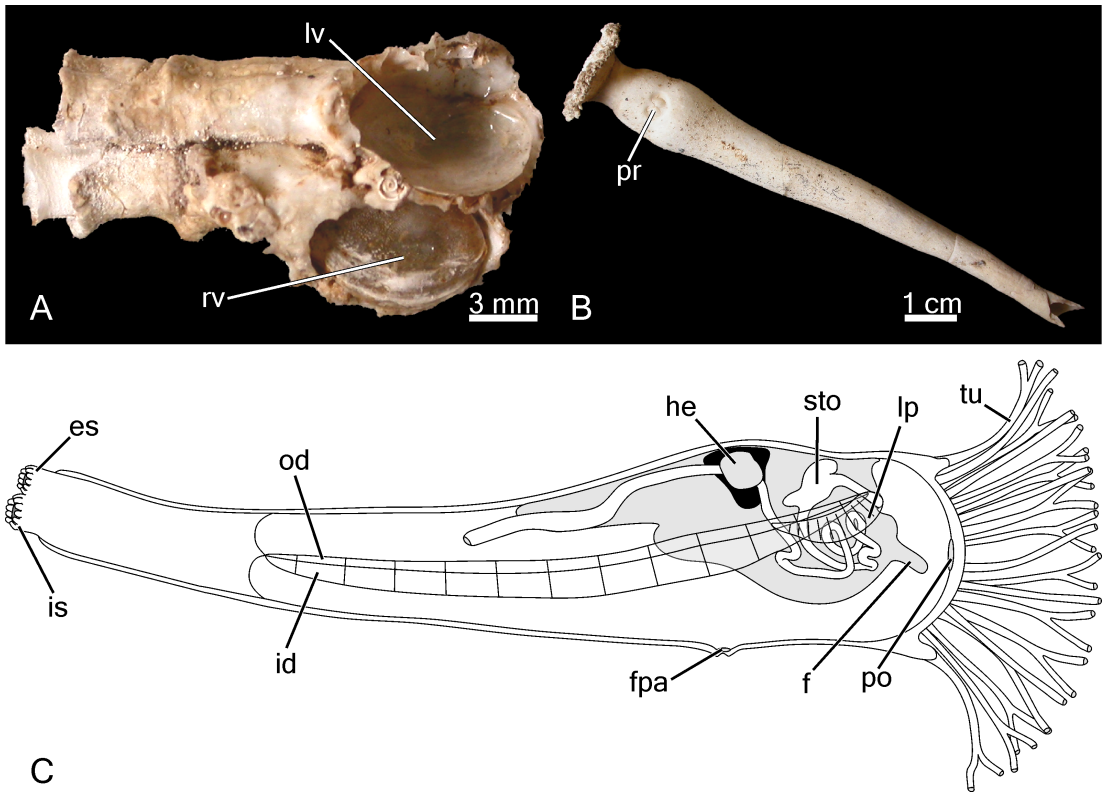


Figure 1.4: Crypt morphology and gross anatomy of extant clavagelloids. **A**. *Dianadema minima*, BMNH 1886.2.10.48. Right view of two specimens cemented together. The anterior portion of the crypt was broken to expose the internal surface of the left shell valve in the top specimen and the external surface of the right valve in the bottom one. **B**. *Aspergillum strangulatum*, BMNH 1841.10.12.28. Dorsal view of the crypt. Anterior end towards the top left corner. **C**. Schematic drawing of the gross anatomy of *Penicillus penis*, after Lacaze-Duthiers (1883). Abbreviations: **es**, exhalant siphon; **f**, foot; **fpa**, fourth pallial aperture; **he**, heart; **id**, inner demibranch; **is**, inhalant siphon; **lp**, labial palp; **lv**, left shell valve; **od**, outer demibranch; **po**, pedal opening; **pr**, primary (juvenile) shell; **rv**, right shell valve; **sto**, stomach; **tu**, anterior tubules (watering pot).

septum or reduced gills regarded as intermediate stages between 'normal' filter-feeding ctenidia and the septum (Fig. 1.5). The three families recognised by Keen (1969*a*) and Morton (1981*b*), Verticordiidae, Poromyidae and Cuspidariidae, are cosmopolitan and most abundant and diverse in bathyal and abyssal depths, although a few representatives of each also occur in shallower water (Krylova, 2001; Simone & Cunha, 2008). Except for *Dilemma*, a recently described genus of epibyssate poromyids (Leal, 2008; Sasaki & Leal, 2008), all septibranchs are either shallow burrowers or endobyssate.

Contrary to the pholadomyoid family Parilimyidae, for which an inferred carnivorous diet remains unproven, analyses of stomach contents provide direct evidence of carnivory in septibranchs, with a wide diversity of ingested items being recorded, including

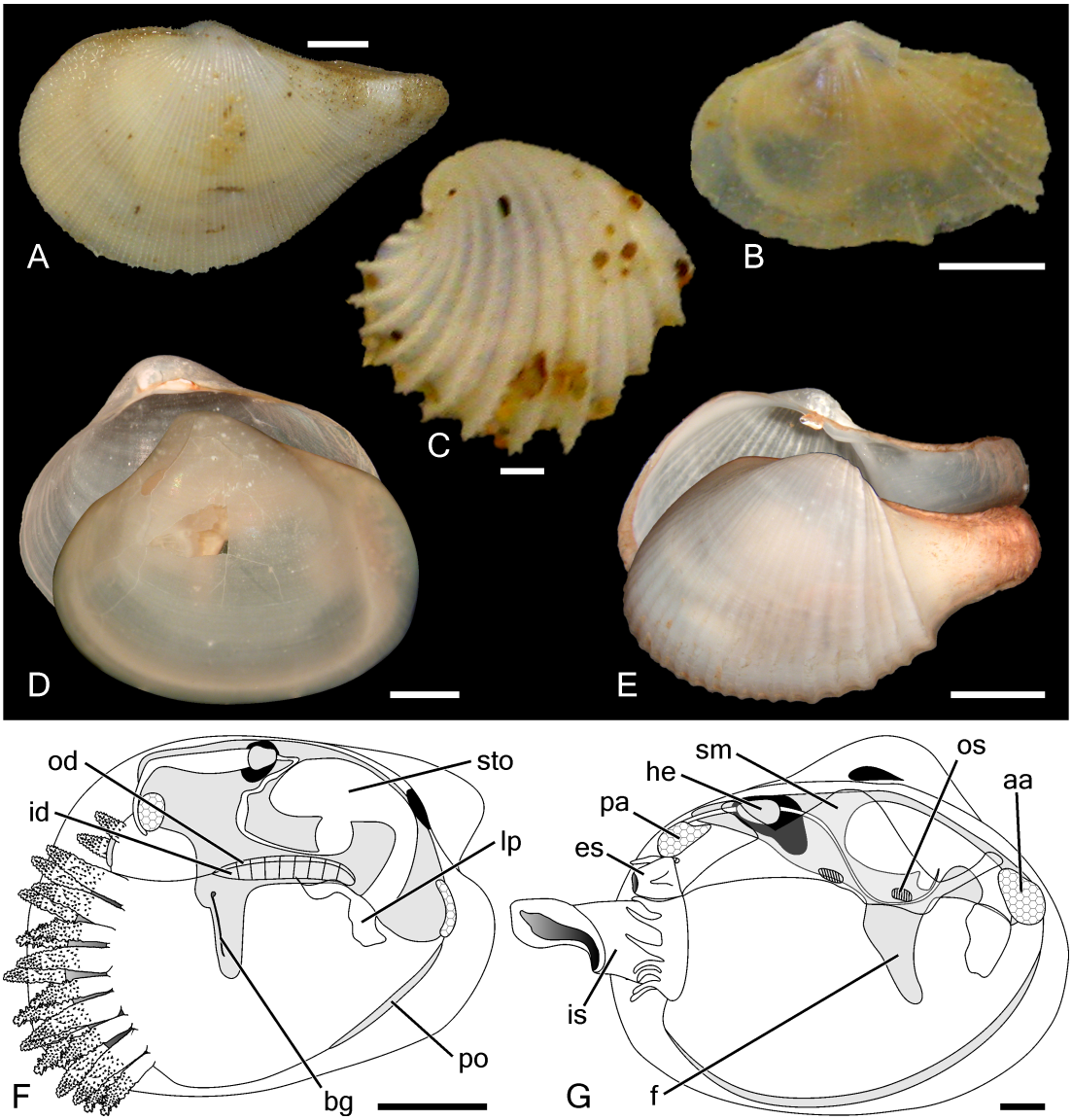


Figure 1.5: Shell morphology and gross anatomy of extant septibranchs. **A**–**E**. Left view of the shell of the euciroid *Acreuciroa rostrata*, lyonsiellid *Lyonsiella* cf *formosa*, verticordiid *Spinosipella deshayesiana*, poromyid *Poromya tornata* (all MNHN, unregistered) and cuspidariid *Cardiomya cleryana* (CENEMAR, unregistered; Santos, SP, to São Francisco do Sul, SC, Brazil), respectively. **F** and **G**. Schematic drawings of the gross anatomy of the lyonsiellid *Lyonsiella abyssicola* (after Allen & Turner, 1974) and poromyid *P. tornata* (after Allen & Morgan, 1981), respectively. Abbreviations: **aa**, anterior adductor muscle; **bg**, byssal groove; **es**, exhalant siphon; **f**, foot; **he**, heart; **id**, inner demibranch; **is**, inhalant siphon; **lp**, labial palp; **od**, outer demibranch; **os**, septal ostia; **pa**, posterior adductor muscle; **po**, pedal opening; **sm**, septum; **sto**, stomach. Scale bars: **A** = 6 mm; **B**, **D** and **E** = 3 mm; **C**, **F** and **G** = 1 mm.

forams, worms (polychaetes, oligochaetes, nematodes and chaetognaths), crustaceans, bivalves, gastropods and fish scales (Knudsen, 1967, 1970; Bernard, 1974; Krylova, 2001). Additionally, *in vivo* observations of cuspidariids (Reid & Reid, 1974; Reid & Crosby, 1980) have shown that members of at least this family are able to predate on active, swimming prey, rather than being strictly scavengers.

There are significant morphological differences among septibranchs which have entertained numerous re-evaluations of the traditional division in three familial groups featured in the *Treatise*. This has led to a proliferation of distinct classificatory schemes, commonly involving changes of rank of the three major divisions (e.g. by Morton, 1982, 1985*a*), split of each into several distinct families or subfamilies (e.g. by Poutiers & Bernard, 1995; Krylova, 2001) and/or inclusion of dubious fossil taxa in the group (e.g. by Scarlato & Starobogatov, 1983; Starobogatov, 1992; Nevesskaja, 2009). However, most of these changes have been ignored or challenged by subsequent authors. Only the referral of some verticordiids to two separate families, Lyonsiellidae and Euciroidae, has been commonly adopted (e.g. Morton, 2003*b*; Harper *et al.*, 2006).

In recent years, Marshall (2002) suggested that the poorly known extant family Spheniopsidae, known only from conchological material and considered by most authors to have myoid affinities (e.g. Coan, 1990*a*), may belong to Anomalodesmata, possibly related to Cuspidariidae. Marshall's (2002) proposal, justified on the basis of similarities in shell outline, sculpture and ligament structure between the spheniopsid genus *Grippina* and cuspidariids, requires anatomical confirmation but has been incorporated in at least some bivalve classifications (e.g. Bieler & Mikkelsen, 2006; Mikkelsen & Bieler, 2008).

1.2 Search for phylogenetic relationships

Anomalodesmatan systematics has been historically dominated by authoritative classifications, outlined on the basis of phenotypic similarity, subjective decisions regarding the importance of distinct lines of evidence and often unclear or inconsistent analytical criteria.

Similarly to bivalves in general, throughout the 19$^{\text{th}}$ and well into the 20$^{\text{th}}$ century, anomalodesmatan relationships were studied using a single or few morphological characters, with each author despairing of previous ideas and regarding their chosen taxobasis as a better guide to phylogeny (see Cox, 1960; Newell, 1965, for thorough reviews). It is worth noting that as early as the 1900s, a few authors (e.g. Dall, 1889*a*;

Ridewood, 1903) had noted the inadequacy of these schemes in dealing with cases of homoplastic evolution and highlighted the importance of considering multiple taxobases in drawing classifications. However, the pluralistic approach they advocated was little reflected in their practices, and they too frequently placed great importance on their preferred taxobases while relegating other features to a secondary role. Erection of Anomalodesmata by Dall (1889*a*), for instance, seems to have been solely based on the lack of hinge teeth because he referred to the group not only taxa still included here, but also edentulous superfamilies which are very distinct anatomically (Solemyoidea, Pholadoidea and Myoidea). Significantly, only a few years latter Dall (1895) himself transferred these superfamilies to other groups.

In the second half of the last century taxonomic schemes based on a more eclectic approach, taking into account multiple characters and combining zoological with palaeontological evidence (Cox, 1960; Newell, 1965; Newell *et al.*, 1969*b*; Runnegar, 1974), proved more popular than those which insisted in sole taxobases, epitomised by Purchon's (1959; 1960*a*; 1963) classification established on the basis of internal stomach anatomy. Contemporary views of anomalodesmatan phylogenetic relationships are still largely influenced by such integrative syntheses, elaborated within the framework of traditional, authoritative systematics, in particular those of Newell *et al.* (1969*b*) and Runnegar (1974).

Few objective analyses of bivalve relationships appeared in the years between publication of the *Treatise* and the late 1990s, a period in which cladistics, popularised by the publication of Hennig's work in English (Hennig, 1966), led to significant advances in the study of many other taxa (Schneider, 2001). Three papers featured in the proceedings of a symposium on bivalve systematics are noteworthy exceptions.

The first, by Purchon (1978), consisted of a computer-assited phenetic analysis of bivalve relationships and had the merits of being completely transparent regarding applied methods and assumptions. However, the value of Purchon's (1978) work is downgraded by the inherent flaws of the phenetic approach, specially its inability to distinguish plesiomorphic from apomorphic similarity.

The second and third papers, by Waller (1978) on the relationships of pteriomorphians and Boss (1978) on anomalodesmatans, represented the first attempts to apply principles of cladistics to bivalve systematics. Boss' (1978) analysis focused on the relationships of seven anomalodesmatan families placed in Pandoroidea by Newell (1965) and proposed to split the group into two clades, corresponding to Thracioidea and Pandoroidea of contemporary authors. Despite the success of this study, measured by

its prevalent influence on subsequent syntheses of anomalodesmatan evolution (Yonge & Morton, 1980; Morton, 1981*b*, 1982, 1985*a*; Prezant, 1998*b*), Boss' (1978) analysis lacked objectivity and it is not even entirely clear how many characters were considered.

Only from the late 1990s, cladistic analyses with explicit datasets involving anomalodesmatans were produced. The vast majority of these consisted of morphological (von Salvini-Plawen & Steiner, 1996; Waller, 1998; Carter *et al.*, 2000), molecular (Adamkewicz *et al.*, 1997; Campbell, 2000; Steiner & Hammer, 2000; Giribet & Distel, 2003; Taylor *et al.*, 2007) and combined (Giribet & Wheeler, 2002) analyses aiming at resolving relationships among high-level bivalve taxa (superfamilial and ordinal levels). As such, they were valuable in elucidating the sister-group relationships of Anomalodesmata, but included too few representatives of the group to adequately test its monophyly or to give meaningful insights as to the interrelationships of the component families. The morphological study of Harper *et al.* (2000), and the molecular investigations of Dreyer *et al.* (2003) and Harper *et al.* (2006) represent the only modern cladistic analyses primarily concerned with extant anomalodesmatans. The impact of these investigations on our understanding of anomalodesmatan phylogenetic relationships will be briefly discussed in the sections below.

1.2.1 Sister group relationships and monophyly of Anomalodesmata

Until the recent adoption of molecular techniques of phylogenetic inference, the relationships between Anomalodesmata and other bivalve higher taxa were submerged in controversy. Although by far the most frequently advanced proposal had been of a close relationship between anomalodesmatan and myoid taxa (e.g. Taylor *et al.*, 1973; Runnegar, 1974; Purchon, 1978; Carter, 1978, 1990; Morris *et al.*, 1991; Morton, 1996; von Salvini-Plawen & Steiner, 1996), affinities to protobranchs (e.g. Purchon, 1956; Runnegar, 1974), pteriomorphians (e.g. Pojeta & Runnegar, 1985; Starobogatov, 1992; Carter *et al.*, 2000) and palaeoheterodonts (e.g. Cope, 1997) were also entertained. Waller (1998) argued for a monophyletic heteroconch clade joining Palaeoheterodonta, Heterodonta and Anomalodesmata, but did not discuss relationships within this group. In a previous study, he had presented a cladogram in which a clade joining Anomalodesmata and Heterodonta was depicted as sister group of Palaeoheterodonta (Waller, 1990, fig. 2).

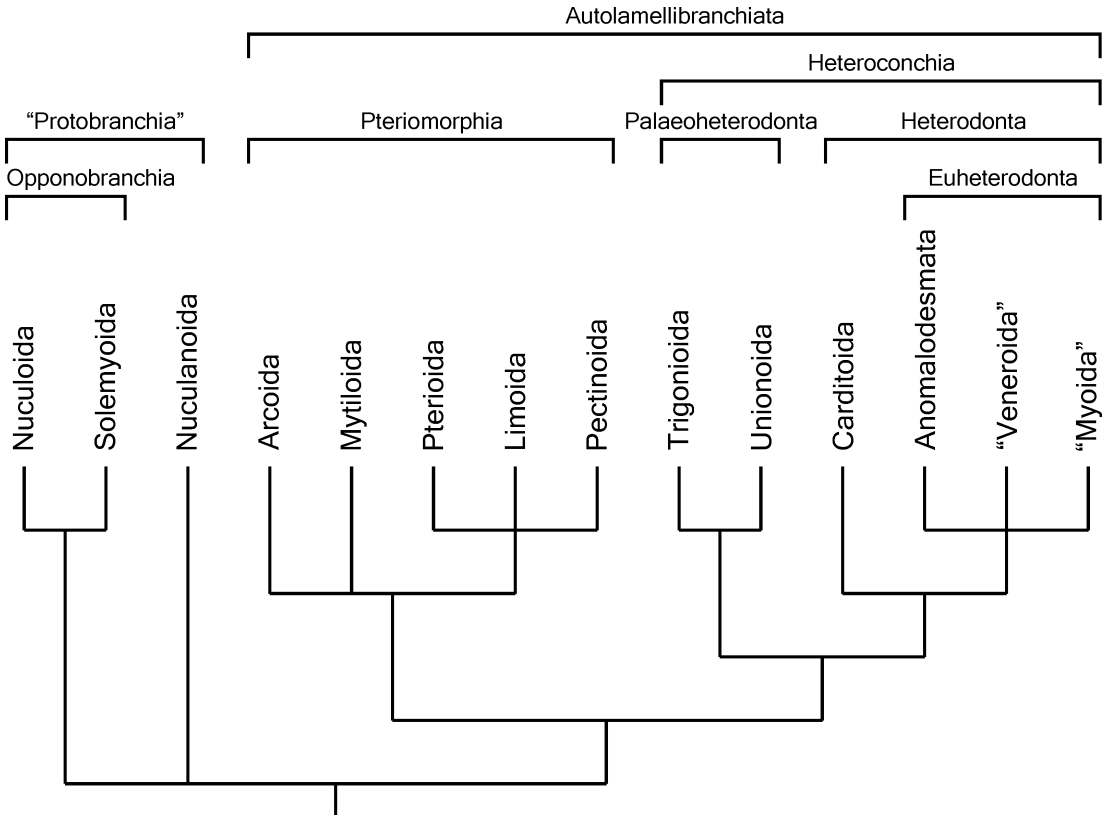


Figure 1.6: Current understanding of phylogenetic relationships among major bivalve groups. Topology of the dendogram is a compromise between recently published cladistic analyses of extant bivalves, as summarised by Bieler & Mikkelsen (2006, fig. 1) and Giribet (2008, fig. 6.8). Taxa surrounded in quotation marks are putatively merophyletic.

Another common practice had been to question the monophyletic status of Anomalodesmata by suggesting transferral of some or all septibranchs close to either protobranchs (Purchon, 1956, 1963; Bernard, 1974; Runnegar, 1974) or myoids (von Salvini-Plawen & Haszprunar, 1982; Healy, 1996), based on similarities in a single or few morphological characters. von Salvini-Plawen & Steiner (1996) tested these proposals by scoring Septibranchia and remaining Anomalodesmata independently in their matrix of 42 morphological characters. The resulting cladogram recovered a monophyletic group linking these two terminals, supported by "presence of a lithodesma, together with other changes in the ligament, as well as the obligatory hermaphroditism" (von Salvini-Plawen & Steiner, 1996, p. 44).

Except for the early 18S rRNA parsimony analysis of Adamkewicz *et al.* (1997, p. 619), which admittedly "could not confidently establish either the monophyly or the phylogenetic relationships of the morphologically well defined subclasses Pteriomor-

phia, Protobranchia, and Anomalodesmata", all molecular and combined analyses of bivalve relationships performed to date nest anomalodesmatans within Heterodonta, a fact now reflected in classificatory schemes (Bieler & Mikkelsen, 2006; Giribet, 2008). These analyses have also recovered monophyletic Anomalodesmata although even the most comprehensive study currently available (Harper *et al.*, 2006) was not able to include representatives of all extant families and superfamilies. While there is general agreement among molecular cladograms that Carditoida comprises the sister group of Euheterodonta (monophyletic Anomalodesmata plus polyphyletic Veneroida and Myoida), resolution of interrelationships within the latter clade remains contentious (Giribet, 2008). Our current understanding of the relationship of Anomalodesmata to other bivalve groups is shown in Figure 1.6.

1.2.2 Relationships within the Anomalodesmata

If, at least as far as extant representatives are concerned, there is currently little doubt about the monophyletic status of Anomalodesmata and significant advances have been made to unravel the position of the clade in the bivalve tree of life, on the other hand relationships within the group remain highly contentious.

Pholadomyoidea is generally regarded as the most plesiomorphic not only due to its longevity, but also for exhibiting characters traditionally regarded as primitive for anomalodesmatans, including a nacreo-prismatic shell and parivincular ligament. Many have suggested more or less directly that Pholadomyoidea contain the ancestors of all other modern anomalodesmatans superfamilies (e.g. Runnegar, 1974; Morton, 1981*b*, 1985*a*; Morris *et al.*, 1991), being therefore a merophyletic group of convenience. Based on these views, Harper *et al.* (2000) chose *Pholadomya candida* as outgroup in their cladistic study of extant anomalodesmatans. Contrary to suggestions by Morton (1982, especially fig. 43) and Poutiers & Bernard (1995) that Parilimyidae might be more closely related to septibranchs than to Pholadomyidae, Harper *et al.* (2000) found *Pholadomya* and *Parilimya* closely related. Molecular studies have so far failed to sample pholadomyoids, although efforts are under way to sequence both parilimyids and *P. candida* (Diaz *et al.*, 2009).

As commented above, the only modification to Newell *et al.*'s (1969*b*) superfamilial divisions of Anomalodesmata to find its way into virtually all subsequent treatments of the group was the split of Pandoroidea initially proposed by Boss (1978) in his early cladistic study. Boss (1978) also attempted to resolve relationships within each

child clade, pointing Thraciidae as the sister group of Laternulidae plus Periplomatidae within Thracioidea, and putting forward two distinct hypotheses for Pandoroidea, whose consensus is shown in Figure 1.7A. Morton (1996, fig. 29.9) placed Pandoroidea and Pholadomyoidea as sister groups in his "evolutionary tree" of Bivalvia. Harper *et al.*'s (2000) analysis recovered monophyletic Thracioidea and Pandoroidea but not a clade joining these two groups (Fig. 1.7B). It also supported Boss' (1978) opinion of a sister group relationship between laternulids and periplomatids, but not of a clade joining Cleidothaeridae and Myochamidae within Pandoroidea.

Surprisingly, the 18S rRNA analyses of Dreyer *et al.* (2003) and Harper *et al.* (2006) refuted the monophyly not only of Thracioidea and Pandoroidea (Fig. 1.7C), but also of a larger clade uniting these groups (Pandoroidea *sensu* Newell *et al.*, 1969*b*). As noted by Harper *et al.* (2006), this part of the anomalodesmatan tree had been widely regarded as the most stable and not contentious. Instead, Dreyer *et al.* (2003) and Harper *et al.* (2006) recovered a "thraciid" clade joining thraciids, cleidothaerids and myochamids, as well as a "lyonsiid" clade comprising laternulids, lyonsiids, pandorids and clavagellids. Except for Thraciidae and Lyonsiidae, all these families were found monophyletic (Fig. 1.7C).

The relationships of clavagelloids have proved particularly difficult to resolve from a morphological point of view due to the lack of known intermediate forms both among the distinct clavagelloid lineages and between the group as a whole and the remaining anomalodesmatans. Based on conchological and anatomical features Taylor *et al.* (1973) and Carter (1978) suggested relationships with pandoroids, the latter author emphasising the significance of presence, then still debatable, of a lithodesma in both groups. On the other hand, Morton (1981*b*, 1984*a*,*b*, 1985*a*) claimed the origins of the group should be sought among Pholadomyoidea, and Pojeta & Sohl (1987) narrowed this possibility down to Pholadomyidae due to similarities between clavagellid larval shells and pholadomyid adult shells. Harper *et al.*'s (2000) analysis recovered a rather unexpected sister group relationship between monophyletic clavagelloids and septibranchs, a hypothesis which had only been previously presented albeit not discussed by Morton (1996, fig. 29.9). Molecular analyses similarly supported monophyly of Clavagelloidea (Harper *et al.*, 2006), but indicated a more orthodox lyonsiid sister group instead (Dreyer *et al.*, 2003; Harper *et al.*, 2006).

Septibranchs were the first known example of bivalve carnivory (Pelseneer, 1891*a*) and, driven by the allure of this unusual diet, many have attempted to elucidate their

origins and interrelationships. One of the earliest and perhaps the most prevalent hypothesis of septibranch evolution has been of a trend toward reduction and muscularisation of the gills, with verticordiids representing a link between other anomalodesmatans (particularly pandoroids or even more specifically lyonsiids) and the more specialised families Poromyidae and Cuspidariidae (e.g. Pelseneer, 1888*a*; Ridewood, 1903; Allen & Turner, 1974).

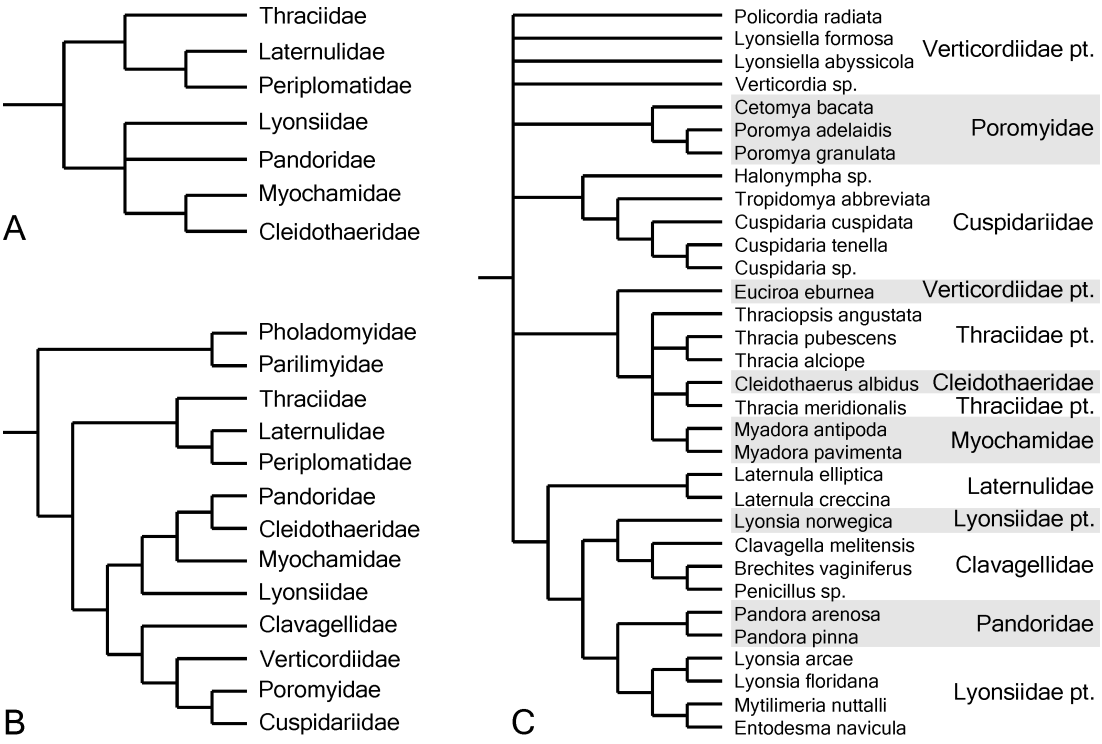


Figure 1.7: Cladistic hypotheses of anomalodesmatan interrelationships. **A**. Consensus of Boss' (1978) views on sister group relationships among extant thracioids and pandoroids. **B**. Familial relationships according to Harper *et al.*'s (2000, fig. 2) "total evidence" morphological tree. **C**. Harper *et al.*'s (2006, fig. 5) 18S rRNA Bayesian tree with familial assignments superimposed.

However, even among authors who agree with derivation of the group from an anomalodesmatan ancestor, other arrangements have been proposed and several have expressed doubts regarding the monophyly of the three contained families. Hence, Ridewood (1903) and Yonge (1928) recognised Septibranchia as a probably natural grouping but suggested poromyids and cuspidariids might have evolved convergently; Bernard (1979) regarded Cuspidariidae as the sole monophyletic septibranch group and speculated that they might have arisen from Permian Edmondioidea; Allen & Morgan (1981) concluded on anatomical grounds that Verticordiidae and Poromyidae are more closely related to one another than either is to Cuspidariidae; Morton (1982,

1987*a*) considered that each family may have arisen independently from a pholadomyoid ancestral similar to *Parilimya*; and Morris *et al.* (1991) expressed doubt in determining whether or not the fossil family Megadesmidae may be ancestral to at least some septibranchs.

The diversity of opinions among authors who have sought derivation of Septibranchia from outside Anomalodesmata is similarly wide and classifications which, impressed by their highly modified anatomy and using phenetic criteria, regard the group as a major subdivision of Bivalvia (equal in rank to Protobranchia and Autolamellibranchiata) still find expression in the recent literature (e.g. Nevesskaja, 2009).

Harper *et al.* (2000)'s cladogram corroborated the prevailing hypothesis of Poromyidae and Cuspidariidae more closely related to one another than each to Verticordiidae within a monophyletic septibranch clade, and strongly supported monophyly of Verticordiidae, the only carnivorous family represented by two taxa (Fig. 1.7B). Dreyer *et al.* (2003) and Harper *et al.* (2006) supported the monophyly of Poromyidae and that of Cuspidariidae only when a dubious sequence of *Myonera* sp. was excluded from analyses. Monophyly of Verticordiidae or Septibranchia as a whole was neither supported nor rejected because *Euciroa* clusters with the "thraciid" clade albeit with low branch support, and the remaining septibranch branches are involved in a basal polytomy with "thraciid" and "lyonsiid" clades (Fig. 1.7C).

In summary, anomalodesmatan phylogeny remains an enigma and our understanding of their evolution is in its infancy. Significantly, familial interrelationships suggested by the most recent and comprehensive morphological (Fig. 1.7B) and molecular (Fig. 1.7C) cladograms of the group are strikingly different.

1.3 Aims and outline of the present study

The aims of this investigation are to:

1. conduct an exhaustive survey of all major organ systems within the Anomalodesmata, with the specific objectives of:
    - re-assessing hypotheses of primary homology in the light of evidence pointing to heterodont taxa as immediate outgroups of the clade; and
    - gaining a better understanding of the distribution and variation of morphological features within each nominal family.

2. subject the resulting dataset to cladistic analyses, testing:

   - whether differences between authoritative classifications and cladistic analyses of Anomalodesmata may be explained, at least in part, by the use of plesiomorphic or homoplastic character states as diagnostic features of nominal groups in traditional systematic studies; and
   - if the marked incongruence between morphological and molecular cladograms of the group might be mitigated by increased taxonomic sampling and more rigorous character analyses.

3. discuss some aspects of the evolutionary history of Anomalodesmata in the light of the new findings.

Because the hinge ligament has been regarded as the most important taxobasis in discussions of the systematics and evolution of the clade, the organ is a logical starting point for a re-examination of anomalodesmatan morphology. In chapter 2, a detailed study of the structure and development of one of the most complex ligament systems displayed by extant representatives of the group sets the basis for a comparative survey, which results in a new model for the evolution of anomalodesmatan ligament grades.

Chapter 3 focuses on the arenophilic system, a network of multicellular pallial glands with a dedicated function in sediment agglutination. These organs comprise one of the only anatomical features that is exclusive of anomalodesmatans, but which has been commonly neglected for being relatively difficult to detect. I set out to show that the glands are present in a larger ensemble of taxa than previously realised and that their presence may be indirectly determined by characteristic lines of secretion on the external shell surface of both extant and exceptionally preserved fossil material.

All other major conchological and anatomical characters are discussed in chapter 4, which sets the basis for the largest cladistic analysis of extant anomalodesmatans performed to date, presented in the final analytical chapter of this volume (chapter 5).

In chapter 6, I briefly review the fossil record of Anomalodesmata and apply stratigraphic data to move from competing cladograms to a tentative phylogeny of extant familial groups. Ancestor-descendant relationships and trends in the post-Palaeozoic evolutionary history of the clade are discussed in the light of the proposed phylogeny.

Chapter 2

Structure and development of the anomalodesmatan ligament

Explaining the importance of hinge characters for bivalve systematics is hardly necessary. One needs only to find Palaeotaxodonta, Palaeoheterodonta, Heterodonta and the whole legion of other "dontas" in a mainstream classification of the group to realise that hinge characters, especially teeth, are very important indeed.

However, the vast majority of anomalodesmatans are edentulous and thus another hinge structure, the ligament, has played the central role in their systematics. In what is perhaps the most influential revision of the group to date, Runnegar (1974, p. 906) notes that "Except for the bizarre Clavagellacea, the Subclass Anomalodesmata can be divided into four superfamilies using only two criteria; the nature of the ligament, and the structure of the gills". And in another significant treatment of the group Morton (1981*b*, p. 49) declares that "All agree that the ligament is of prime taxonomic importance in the Anomalodesmata (Yonge, 1978; Runnegar, 1979; Yonge & Morton, 1980) and it is this structure which affords valuable clues as to the origins of the various anomalodesmatan lineages".

The view that ligament structure offers the best taxobasis for anomalodesmatan systematics is attributable in part to the observation of a stratigraphic sequence leading from external to internal ligaments and in part to the conclusions of detailed studies of ligament morphology in extant forms.

Most early anomalodesmatans possessed external ligaments supported by nymphs (i.e. *parivincular*) and, in fact, before the studies of Cope (1996*a*) and Sánchez & Vaccari (2003) suggested there might have been Ordovician anomalodesmatans with an internal ligament, it was believed that all Palaeozoic anomalodesmatans had the

ligament in an external position (Morris *et al.*, 1991). Subsequently, in the Mesozoic and Cenozoic, some representatives of the group evolved subinternal and internal ligaments (Cox, 1963; Newell *et al.*, 1969*a*) and, based on these observations, Runnegar (1974) envisaged the evolution of anomalodesmatan ligament systems as a process of ventral migration of the entire structure below the hinge line.

This process of ventral migration was deemed irreversible following the pronouncements of Yonge (1976) and Yonge & Morton (1980) that the internal ligament supported by a calcified ossicle is too complex to have evolved iteratively. As Yonge (1976, p. 405) summarises "Because so very distinctive a type of ligament is most unlikely to have evolved more than once, its presence provides unusually convincing evidence of the close relationship of all bivalves that possess it".

With a few exceptions which will be discussed in the following sections, subsequent studies of the clade echoed the above conclusions and anomalodesmatan higher groups (superfamilies and families) are still largely defined on the basis of ligament characters. Hence, failure to recover these higher groups in cladistic analyses (e.g. Dreyer *et al.*, 2003; Harper *et al.*, 2006) may offer a valuable indication that ligament evolution has been more homoplastic than currently realised.

This chapter reviews ligament structure in extant anomalodesmatans and reveals significant drawbacks in the prevailing hypothesis for the evolution of the organ. An alternative model is proposed which derives each type of anomalodesmatan ligament mostly from heterochronic changes of a primitively disjunct ligament system. The new model is based on detailed observations of a relatively complete post-larval growth series of *Thracia phaseolina* (Lamarck, 1818), which possesses a complex adult ligament comprising both internal and external portions, and a comparative study of juveniles and/or adults of all extant anomalodesmatan superfamilies. Observations on *T. phaseolina* are published in Sartori & Ball (2009).

2.1 Definitions

I follow the terminology of Trueman (1969), revised by Waller (1990), Carter (1990) and Malchus (2004) regarding ligament morphology, layers, systems and support structures.

The terms *lamellar* and *fibrous* refer to ligamental layers differing in composition and physical properties (e.g. Figs 2.4A and 2.8I). Lamellar ligament is characteristically dark brown, uncalcified and resistant to both tensional and compressional stresses. Fibrous ligament is lighter in colour, often iridescent, filled with fine aragonitic fibres,

and resistant only to compressional stress. Morphologically simple ligaments have a central fibrous layer between anterior and posterior lamellar layers. *Multiple* ligaments display additional layers.

Following Malchus (2004), successive ligamental layers are designated a letter corresponding to their kind (F for fibrous and L for lamellar) and a number according to their putative ontogenetic order of appearance ($1, 2 \ldots n$). Thus, F1 represents the first formed fibrous layer, F2 the second, and so on.

Parivincular describes a dorsal, arch-shaped ligament, which is positioned posterior to the umbones and supported by a well-defined ridge (nymph) in each valve (e.g. Figs 2.7A and 2.8I).

Lithodesma is a solid structure formed by calcification of the medial portion of a ligament layer (Yonge, 1976). The same layer also comprises two lateral strips of unmodified ligament that attach to the shell valves (e.g. Figs 2.3A and 2.6).

2.2 Material and Methods

2.2.1 Detailed study of *T. phaseolina*

Specimens of *T. phaseolina* were collected on 9 and 20 August 2007 from the Ría de Ferrol, Galícia, Spain (J. M. da Rocha, personal communication 2007). Seven catches of a Van Veen grab (0.056 m^2 each) in fine sand substrata at approximately 6 metres depth yielded 86 intact specimens ranging from 1.34 to 12.7 mm in shell length. Two additional specimens (8.14 and 22.2 mm in shell length) were collected on 28 September 2007 from Mill Bay, Kingsbridge Estuary, Devonshire, UK (National Grid Reference SX 742 382; 50°13'30"N 4°45'55"W). They were obtained by shovelling and sieving (through a 1 mm mesh) in sand with patches of eel seagrass *Zostera* sp., at extreme low water of a 0.33 m spring tide. Specimens from both locations were preserved in 80-100% ethanol.

2.2.1.1 Measurements and Allometric Analysis

Lengths of the shell (sl) and fibrous layer of the parivincular ligament (pl), as well as the length (il) and width (iw) of the internal ligament were measured to the nearest 0.02 mm using a stereo-microscope equipped with an ocular micrometer (see Fig. 2.1). Specimens whose shell length exceeded the field of view of the microscope (> 10 mm) had this dimension measured to the nearest 0.1 mm using vernier callipers.

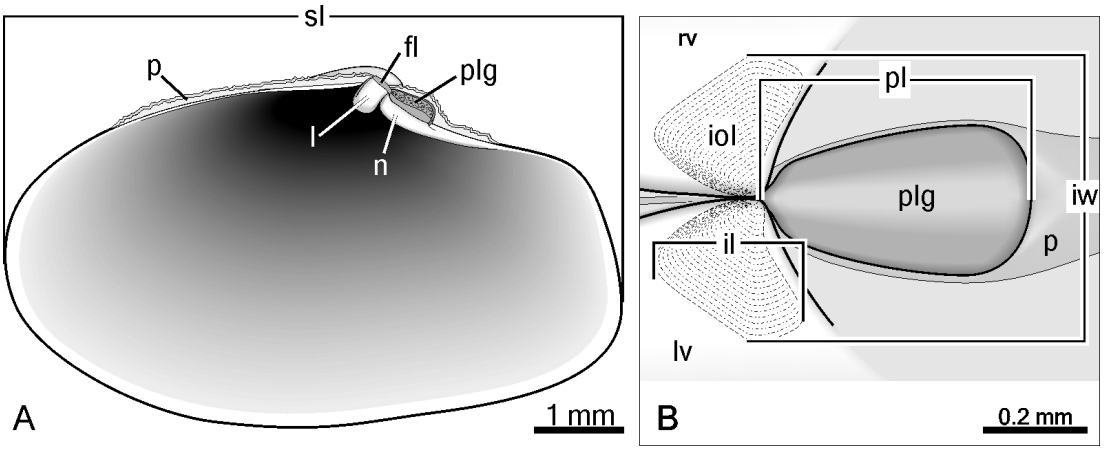


Figure 2.1: *T. phaseolina*. Line drawings showing the main components of the hinge of the species and measurements taken from each specimen. **A**. Internal view of the right valve. **B**. External, dorsal view of the hinge of an articulated specimen. Anterior end towards the left-hand side. Abbreviations: **fl**, resilient part of the internal ligament; **il**, length of the internal ligament; **iol**, outline of the internal ligament, visible through the thin shell in external view; **iw**, width of the internal ligament; **l**, lithodesma; **lv**, left shell valve; **n**, nymph; **p**, periostracum; **pl**, length of the parivincular ligament; **plg**, parivincular ligament; **rv**, right shell valve; **sl**, length of the shell.

The umbonal region of the valves of *T. phaseolina* is translucent when submerged in liquid, allowing the outline of the internal ligament to be clearly seen through the fine shell. Hence, all measurements were taken in external view from intact specimens, with the valves articulated and closed. Although refraction at the convex surface of the umbones must have slightly deviated measurements of the internal ligament from true dimensions, the error thus introduced is approximately the same for all specimens and hence negligible for the purposes of my analysis.

Dimensions of the internal and external (parivincular) portions of the ligamental apparatus relative to body size were studied by non-linear regression of the measured variables *il*, *iw* and *pl* on shell length (*sl*), using Marquardt-Levenberg least-squares algorithm implemented by SigmaPlot 10. Two- ($y = bx^a$) and three-parameters ($y = bx^a + c$) power functions were fitted to the data and their performance assessed by comparing values of adjusted R^2 and Predicted Residual Error Sum of Squares (PRESS), techniques that penalise models containing extra explanatory terms. The investigated models can be reduced to the simpler forms of a linear regression or a two-parameters power function if the values of a and c are equivalent to 1 and 0, respectively. These hypotheses were tested by two-tailed t-tests for each ligament component and rejected whenever the p-value obtained was higher than 0.05.

Scatter plots of the observed values of the ratios il/sl, iw/sl and pl/sl versus sl are also presented, but regression analyses were not performed for these relationships due to the well-known statistical shortcomings of having the same variable represented in both axes of a plot (Prothero, 1986; Berges, 1997). Instead, curves displayed in these plots were drawn by algebraic transformation of the lines of best fit derived from regression of the untransformed variables (il, iw and pl) on total shell length (sl), yielding the equations $y/x = bx^{a-1}$ and $y/x = bx^{a-1} + cx^{-1}$ for the two- and three-parameters power functions, respectively.

2.2.1.2 Functional analysis

To determine whether the internal ligament and associated lithodesma contribute to shell abduction, three specimens showing no traces of a parivincular ligament (shell lengths of 1.51, 1.96 and 2.15 mm) were dissected under a stereo-microscope while completely immersed in 80% ethanol. Tiny insect pins (minutens; 0.1 mm in diameter) were inserted through the commissural line and used to detach all musculature (adductor, pedal, pallial and siphonal) from one of the valves. The capacity to gape of each individual was then qualitatively evaluated by closing their valves with forceps and subsequently releasing the pressure. Following this first experiment, specimens had their lithodesma and most of the internal ligament removed and their capacity to gape re-evaluated.

2.2.1.3 Confocal Microscopy

Taylor *et al.* (2004) used confocal microscopy to discriminate between organic and highly calcified portions of the periostracum of a lucinid bivalve. Because the organic portions showed strong autofluorescence at certain wavelengths whereas the shell wall and calcified portions of the periostracum did not, this physical property could be used to distinguish between these elements.

The resilient portions of the ligament of *T. phaseolina* (lamellar and fibrous layers) similarly display autofluorescence and this property was hence used herein to study the relationship between internal and parivincular components of the ligamental apparatus. A connection between the two elements was sought in both sectioned and decalcified specimens.

Sections through the hinge of air dried specimens were cut using an annular saw operating at 3400 rpm. Sections were oriented parallel to and just off the mid-sagittal

plane, keeping intact the area of maximum proximity between internal and parivincular ligaments.

Decalcified samples were prepared by immersing whole specimens in 0.25% acetic acid until the valves were completely decalcified (typically 2–4 hours), excising the hinge area with dissecting scissors, dehydrating in an ethanol series, washing in xylene and mounting onto cavity microscope slides with a permanent mounting medium.

Both kinds of samples were examined using a Leica TCS NT SP1 confocal microscope. This microscope has a spectral photometer (SP) head which allows the fluorescence detection windows to be set to any desired wavelength and bandwidth, including direct collection of a reflected laser signal. To determine the optimum fluorescence detector settings a lambda (wavelength) scan was performed at two different laser settings across a range of detector positions. The data from these tests were used to produce graphs of maximum fluorescence emission from regions of interest in the sample at one focal plane. 488 nm lambda data was collected using the RSP500 filter and 30 lambda steps from 515 nm to 710 nm with a window width of 10 nm. With these settings a maximum emission peak at 540 nm was obtained. 568 nm lambda was collected using the 488/568 double dichroic mirror and 25 lambda steps from 586 nm to 710 nm with a window width of 10 nm. These settings showed an emission peak at 646 nm. This latter setting was determined to give a better signal to noise ratio in the sample and excited fluorescence from the same part of the sample.

The samples were examined using either a 40x 1.0n.a. oil immersion objective or a 63x 1.4n.a. oil immersion objective. The blocks were temporarily mounted onto glass slides using "BluTak". Care was taken to ensure the upper surface was horizontal. Immersion oil was used to temporarily fix a standard-thickness coverslip in place and the samples were examined under immersion oil using the same objective lenses as for the slides.

2.2.1.4 Scanning Electron Microscopy (SEM)

All specimens selected for SEM were ultrasonically cleaned for 20 seconds, air-dried for 48 hours and gold-coated prior to examination in a JEOL 820 SEM. These included isolated valves and lithodesmas, some of which treated in dilute commercial bleach for 1-2 hours to remove organic matter, as well as radial sections through the internal ligament. The latter were obtained by cutting samples embedded in polyester resin, polishing the cut surfaces using a series of carborundum powders and diamond pastes, and etching for 10 seconds in 0.5% hydrochloric acid.

2.2.2 Comparative study of other anomalodesmatans

Observations of the morphology of the ligament were made for taxa listed in appendix A, which also provides a guide to institutional abbreviations cited in figure captions.

Examination was primarily by means of a dissecting microscope, with specimens immersed in preservative media (generally 70% ethanol). When required, organic components were removed from the samples by immersion in commercial bleach (dilute sodium hypochlorite) for a few minutes. Measurements were taken using either vernier callipers or an ocular micrometer with a minimum accuracy of 0.1 mm.

Selected specimens were examined under SEM, either whole or sectioned after embedding in polyester resin. Preparation of the samples in these cases followed the procedure outlined above for *T. phaseolina*.

2.3 Post-larval development of the ligament of *T. phaseolina*

2.3.1 Observations

2.3.1.1 Internal Ligament

The ligamental apparatus of early juveniles comprises a single, internal layer of fibrous ligament, positioned immediately under the umbones, and a continuous periostracal sheet that connects the dorsal margins of the left and right valves (Fig. 2.2A, G). The latter extends approximately from the anterior to the posterior adductor muscles.

The internal, fibrous ligament originates just below the posterior portion of the prodissoconch hinge line and grows chiefly in a ventral direction. It is connected to each valve by a triangular attachment area (resilifer) which is practically flush with the overall internal surface of the valves (Fig. 2.3C). As the umbones are splayed apart by accretion at the valve margins (see Stasek, 1963*a*), the internal ligament assumes the shape of an arch bridging distant resilifers. Its mid-sagittal sector is extensively calcified, forming a robust lithodesma in between resilient strips of unmodified fibrous fabric (Fig. 2.3A). The microstructure of the lithodesma is characterised by tiny, elongated crystals, arranged predominantly with their long axes normal to the growth surface. This alignment is particularly clear along and in the immediate vicinity of growth bands (Fig. 2.3B).

All three small specimens (shell length <2.5 mm) which had their musculature experimentally detached from the valves were able to gape while their internal ligament

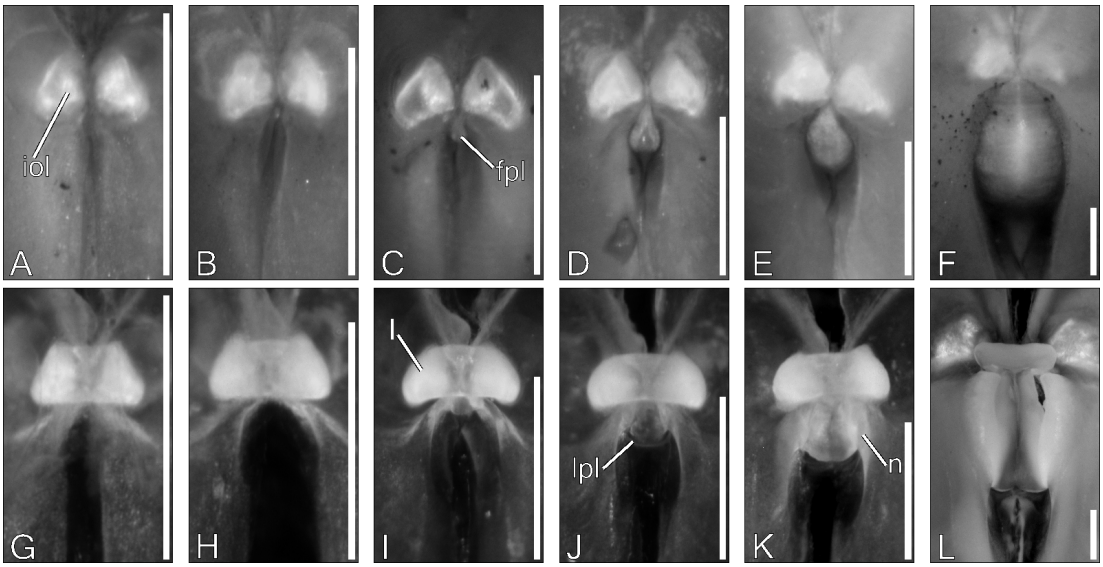


Figure 2.2: *T. phaseolina*. Photographs of dorsal (**A**–**F**) and ventral (**G**–**L**) views of the hinge of a growth series, showing successive stages in the development of the internal and parivincular ligaments. Anterior end towards the top. Abbreviations: **fpl**, fibrous layer of the parivincular ligament; **iol**, outline of the internal ligament, visible through the thin shell in external view; **l**, lithodesma; **lpl**, lamellar layer of the parivincular ligament; **n**, nymph. Length of the shell: **A** and **G** = 2.25 mm; **B** and **H** = 2.88 mm; **C** and **I** = 3.26 mm; **D** and **J** = 3.65 mm; **E** and **K** = 5.00 mm; **F** = 11.3 mm; **L** = 12.72 mm. All scale bars = 0.5 mm

was intact. Subsequent removal of the organ resulted in loss of the capacity to gape, although the valves remained joined by the continuous periostracal sheet along the dorsal margin. These results demonstrate the role of the internal ligament in shell abduction. Most of the opening thrust is presumably generated by the elastic strips of unmodified fibrous fabric that flank the lithodesma. Contributions from the shell walls and lithodesma to the opening thrust must be minimal because these are rigid, inflexible structures.

Calcification of the mid-sector of the internal ligament probably reconciles its unusual, arched profile with the fact that fibrous fabric fails under tensional stress. In most bivalves with an internal ligament (e.g. *Mya*, *Mactra*), the organ sits on projecting supporting structures that not only limit the width of the ligament to a relatively small fraction of its cross-sectional area, but also align its compressional axis along a straight line. When the shell closes, the risk of a ligament of this kind bending and hence having part of its structure subjected to tension is negligible. On the other hand, an internal ligament that is attached directly to the surface of the valves will assume an exceedingly wide and curved profile as the animal grows, with a considerable and

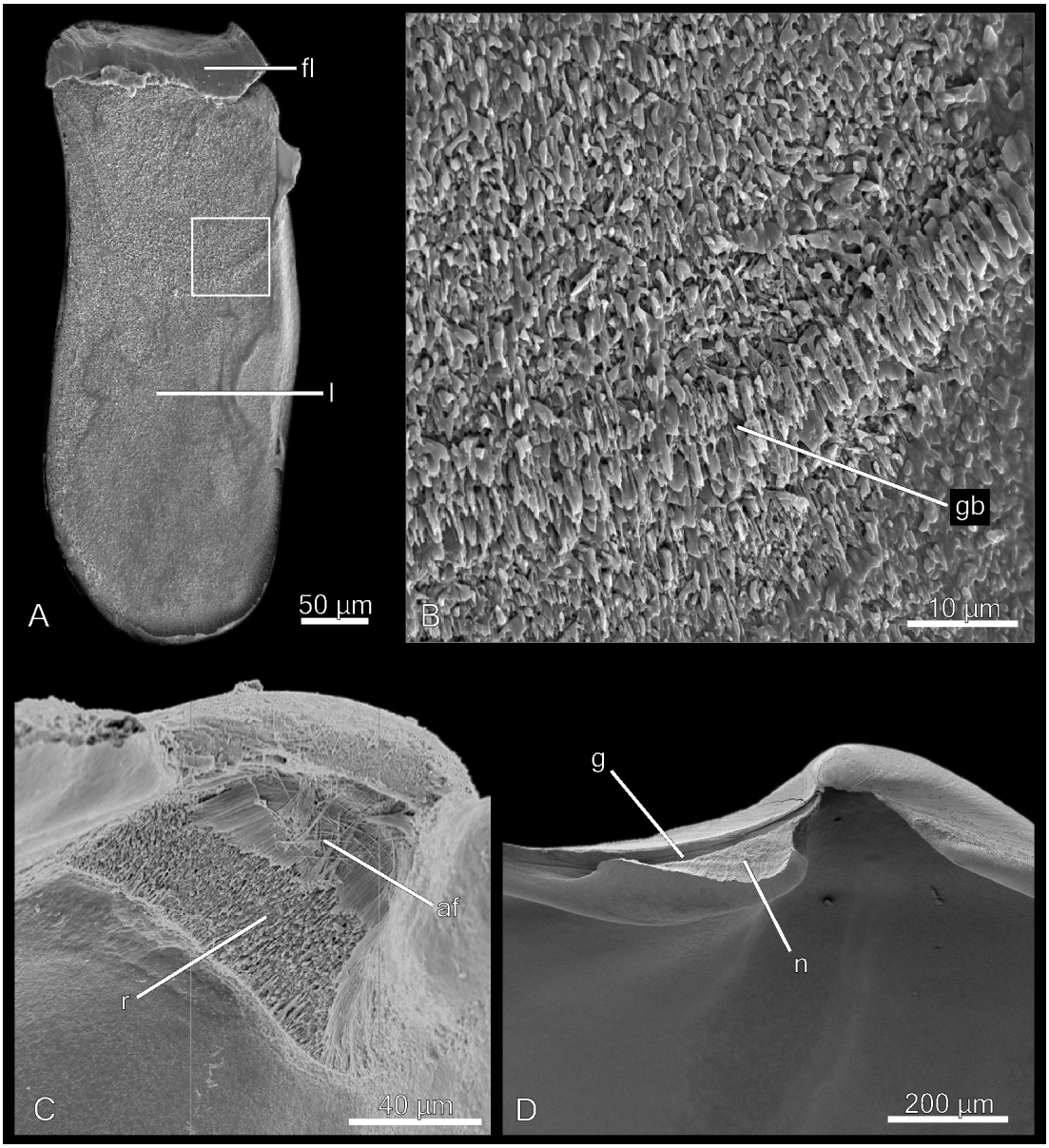


Figure 2.3: *T. phaseolina*. Scanning electron micrographs. **A**. Etched sagittal section through the internal ligament. Anterior margin towards the left-hand side and dorsum towards the top. **B**. Detail of the area delimited by a rectangle in **A**, showing the microstructure of the lithodesma. **C**. Hinge of the right valve of an early juvenile (bleached). **D**. Hinge of the left valve of another bleached specimen. Abbreviations: **af**, aragonitic fibres in a fragment of the internal ligament; **fl**, unmodified, resilient strip of fibrous ligament; **g**, groove occupied by the lamellar layer of the parivincular ligament; **gb**, growth band; **l**, lithodesma; **n**, attachment area of the fibrous layer of the parivincular ligament (nymph); **r**, attachment area of the internal ligament (resilifer). Length of the shell: **A** and **B** = 10.2 mm; **C** = 1.91 mm; **D** = 9.11 mm.

increasing risk of bending upon shell closure. In *Thracia*, deposition of a solid ossicle in the middle of the ligament minimises such risk by dividing the fibrous fabric into two narrow bands with parallel faces, each of which is comparable to the straight internal ligament of other bivalves.

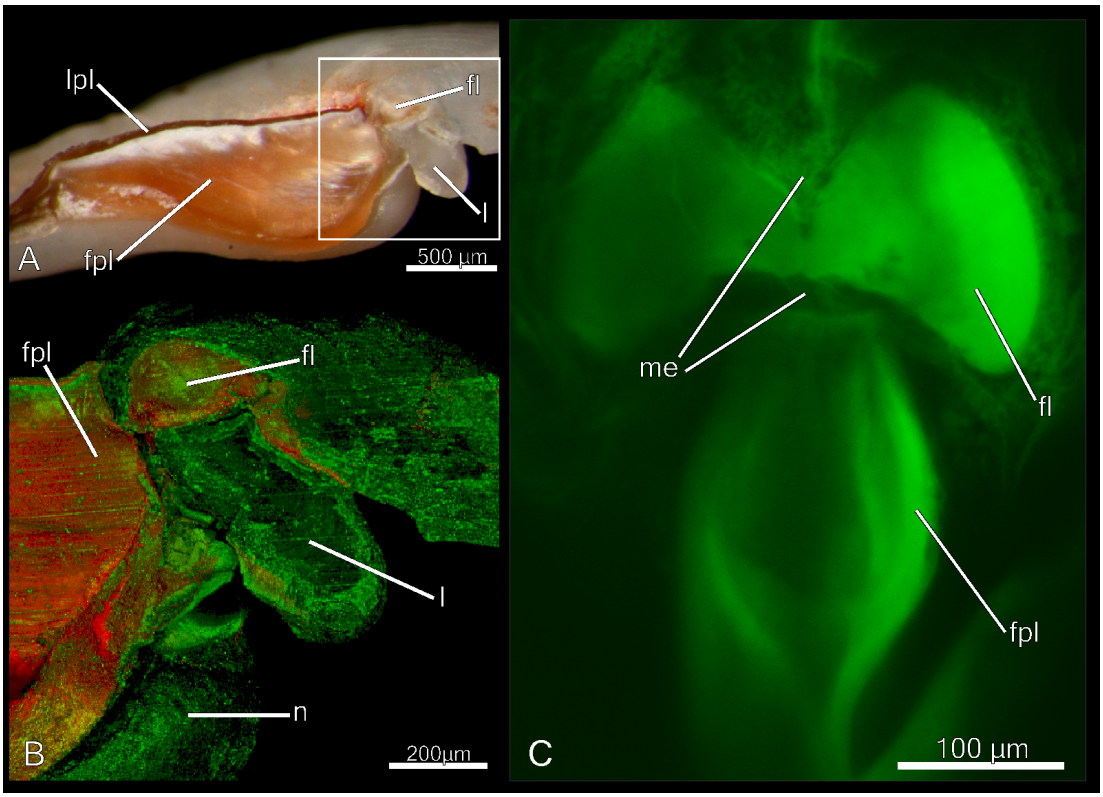


Figure 2.4: *T. phaseolina*. **A**. Radial section through the ligamental apparatus. **B**. Average intensity projection of a stack of 130 images obtained at 2.4 μm intervals from the area delimited by a rectangle in **A**, using a 488 nm argon laser with the 488/568 double dichroic mirror and two detector windows set at 488–507 nm (reflection setting, false coloured in green) and 537–568 nm (fluorescence, false coloured in red). Each frame was scanned twice to obtain an average signal with enhanced signal-to-noise ratio. **C**. Average intensity projection of a stack of 77 images of the hinge of a decalcified specimen, scanned at intervals of 0.8 μm, using the same laser setting as in **B**. However, each frame was scanned four times instead of twice and only the signal from a single detector window (set at 584–676 nm) is shown. **B** and **C** prepared at the Natural History Museum, London, in collaboration with Alexander D. Ball. Abbreviations: **fl**, resilient component of the internal ligament (typical fibrous fabric); **fpl**, fibrous layer of the parivincular ligament; **l**, solid component of the internal ligament (lithodesma); **lpl**, lamellar layer of the parivincular ligament; **me**, mantle epithelium; **n**, nymph. Length of the shell: **A** and **B** = 22.2 mm; **C** = 3.96 mm.

2.3.1.2 Parivincular Ligament

A parivincular ligament and associated nymphs begin to form at a shell length of approximately 2.5 mm. At this stage, the fibrous layer of the parivincular ligament appears at a submarginal position, just posterior to the umbones. It arises very near to the posterior end of the internal ligament, being visible under reflected light as a bright dot in specimens analysed in external, dorsal view (Fig. 2.2B). In internal view, the lithodesma conceals the origination point of the parivincular ligament, making it difficult to determine in whole specimens whether the fibrous layers of the two ligaments are linked together (Fig. 2.2G–L). Sectioned shells and decalcified specimens examined by confocal microscopy clearly show that internal and parivincular ligaments bear independent and discontinuous fibrous layers, separated by a gap of 15.0 μm $\pm$ 5.4 SD (n = 5) (Fig. 2.4). This narrow gap is filled by a tongue of secreting mantle epithelium.

The fibrous layer of the parivincular ligament is separated from the overlying periostracal sheet by a thin, dark brown layer of lamellar ligament, which extends just beyond the anterior and posterior borders of the fibrous layer (Figs 2.2J, 2.4A). The posterior end of the lamellar layer is the most conspicuous, and occupies a shallow depression of the hinge plate. As the nymph grows over the ventral border of this depression, the lamellar layer becomes restricted to a narrow groove in between the nymph and dorsal border of each valve (Fig. 2.3D).

Both layers of the parivincular ligament expand in a predominantly posterior direction. Although the dorsal placement of the lamellar relative to the fibrous layer of the parivincular ligament indicates that the former is secreted first by the mantle isthmus, it was not possible to determine at what shell length the lamellar layer first appears. This is because the lamellar layer is very fine at its origination point near the umbones and displays similar physical properties to those of the overlying periostracum.

2.3.1.3 Allometry

Measurements taken from each specimen are presented in table 2.1. Figure 2.5 illustrates the relationships between total shell length and dimensions of the ligamental apparatus, expressed both as absolute measurements and as proportions of total shell length. The three-parameters power function (solid line, Fig. 2.5) performed better than the two-parameters one (dashed line) in describing changes in width of the internal ligament (*iw*) and length of the parivincular ligament (*pl*) as *T. phaseolina* grows. However, it did not significantly improve the fit obtained by the simpler model for

length of the internal ligament (*il*). This is reflected not only by the results of the *t*-tests, which indicate that the hypothesis of a zero intercept for the curve fitted to *il* cannot be rejected at a 0.05 significance level, but also by adjusted R^2 and PRESS values (Table 2.2).

Table 2.1: *T. phaseolina*. Measurements taken from each individual, in millimetres. All the material was collected from Ría de Ferrol, Spain, except specimens 82 and 88 which were from Mill Bay, UK. Dash indicates absence of a ligament component. Question mark denotes the dimension in question was not measured.

specimen number	shell length	internal ligament length	internal ligament width	parivincular ligament length
1	1.34	0.08	0.13	-
2	1.51	0.09	0.15	-
3	1.91	0.10	0.20	-
4	1.96	0.08	0.19	-
5	1.98	0.11	0.19	-
6	2.15	0.13	0.20	-
7	2.20	0.13	0.20	-
8	2.25	0.13	0.21	-
9	2.25	0.11	0.23	-
10	2.36	0.14	0.24	-
11	2.42	0.14	0.21	-
12	2.42	0.12	0.23	-
13	2.42	0.14	0.25	0.01
14	2.47	0.13	0.20	-
15	2.47	0.14	0.23	-
16	2.53	0.14	0.21	-
17	2.53	0.14	0.24	-
18	2.56	0.12	0.27	0.03
19	2.56	0.14	0.26	0.03
20	2.61	0.15	0.23	-
21	2.67	0.16	0.25	0.02
22	2.81	0.16	0.25	-
23	2.81	0.16	0.27	0.01
24	2.81	0.16	0.24	-
25	2.81	0.15	0.24	0.02
26	2.84	0.15	0.26	0.04
27	2.84	0.17	0.27	0.04
28	2.84	0.17	0.27	0.07
29	2.84	0.15	0.26	0.01
30	2.88	0.13	0.27	0.02
31	2.91	0.14	0.30	-
32	2.91	0.17	0.26	-
33	2.98	0.17	0.27	0.04
34	2.98	0.16	0.28	0.07
35	3.05	0.18	0.28	0.06
36	3.12	?	0.27	0.07
37	3.12	?	0.31	0.08
38	3.12	?	0.32	0.10
39	3.12	?	0.28	0.06
40	3.16	?	0.27	0.07
41	3.19	?	0.30	0.07
42	3.23	?	0.29	0.07

Table 2.1 – Continued

43	3.26	0.14	0.32	0.05
44	3.26	?	0.27	0.07
45	3.26	?	0.33	0.07
46	3.33	?	0.28	0.07
47	3.33	?	0.31	0.13
48	3.44	0.14	0.32	0.10
49	3.44	?	0.33	0.09
50	3.51	?	0.32	0.04
51	3.52	0.14	0.32	0.13
52	3.52	?	0.28	0.13
53	3.61	0.14	0.35	0.13
54	3.65	0.15	0.38	0.14
55	3.65	0.15	0.34	0.15
56	3.65	0.15	0.36	0.16
57	3.74	0.13	0.38	0.17
58	3.74	0.17	0.37	0.17
59	3.74	0.15	0.37	0.20
60	3.83	0.14	0.35	0.19
61	3.83	0.15	0.31	0.14
62	3.83	0.16	0.38	0.14
63	3.83	0.15	0.37	0.15
64	3.87	0.14	0.42	0.20
65	3.91	0.15	0.37	0.15
66	3.91	0.15	0.41	0.12
67	3.96	0.16	0.37	0.23
68	4.00	0.15	0.34	0.16
69	4.00	0.15	0.41	0.13
70	4.00	0.17	0.37	0.20
71	4.04	0.15	0.40	0.20
72	4.22	0.14	0.36	0.23
73	4.22	0.15	0.42	0.14
74	4.30	0.15	0.39	0.22
75	4.35	0.17	0.39	0.20
76	4.56	0.16	0.42	0.19
77	4.61	0.15	0.36	0.23
78	5.00	0.17	0.44	0.20
79	5.00	0.16	0.45	0.28
80	5.56	0.17	0.51	0.30
81	6.86	0.21	0.56	0.55
82	8.14	0.35	0.58	0.67
83	9.11	0.20	0.66	0.70
84	9.44	0.27	0.65	0.80
85	10.2	0.21	0.77	0.73
86	11.3	0.20	0.56	0.92
87	12.7	0.27	0.83	1.16
88	22.2	0.31	1.03	1.73

The better performance of the three-parameters function in describing the allometry of the ligament components, particularly of the parivincular ligament, is a direct result of its non-zero intercept which accommodates shell growth previous to the relative late ontogenetic appearance of the ligamental components. However, the model is

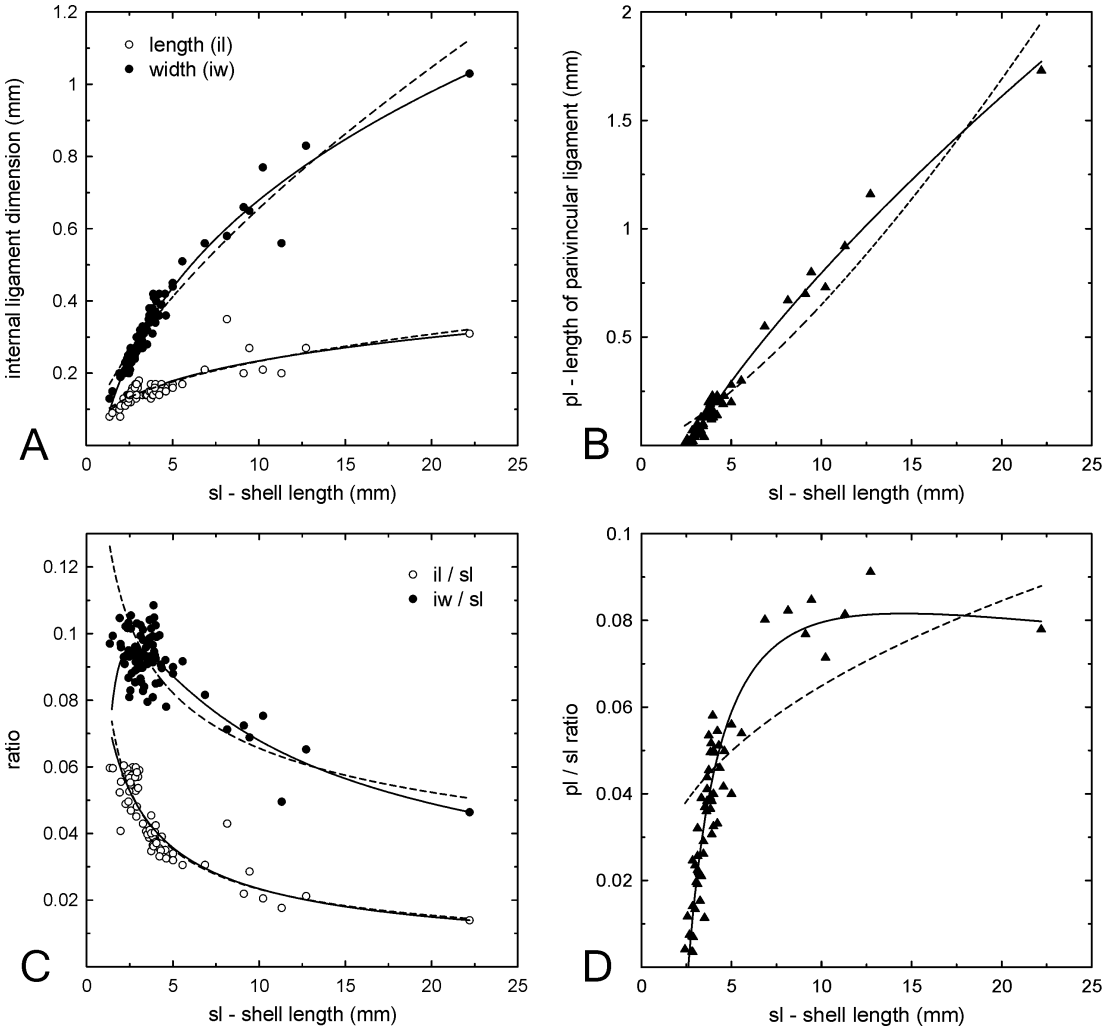


Figure 2.5: *T. phaseolina*. **A** and **B**. Observed values of internal ligament width (iw, •) and lengths of the internal (il, ○) and parivincular (pl, ▲) ligaments plotted against shell length (sl). Solid and dashed curves represent least squares best-fits of the three- and two-parameters power functions, respectively. **C** and **D**. Observed values of the ratios iw/sl, il/sl and pl/sl plotted against sl. Curves represent distributions predicted by the best-fit curves shown in **A** and **B**, algebraically converted to apply to ratios.

rarely used in allometric studies and has been criticised precisely for having a non-zero intercept (e.g. Klingenberg, 1998). A detailed analysis of the properties of the model would deviate focus from the main purpose of this chapter and is thus presented as Appendix B.

Throughout the range of body sizes represented in the sample, the internal ligament displays negative allometry, becoming relatively smaller with increasing shell length (Figs 2.5A, C). Although the three-parameters function predicted an initial increase in

Table 2.2: Summary statistics for regression analyses of width of the internal ligament (iw) and lengths of the internal (il) and parivincular (pl) ligaments on shell length (sl). Two- ($y = bx^c$) and three-parameters ($y = a + bx^c$) power functions were fitted to the data and their performance compared by adjusted R^2 (higher score indicates a better model) and PRESS (lower score indicates a better model). p-values calculated via two-tailed t-tests for each estimate of a and c are shown in brackets.

			Parameters				
Variable	N	Equation	a ($H_0 : a = 1$)	b	c ($H_0 : c = 0$)	Adj. R2	PRESS
il	74	$il = b\,sl^a$	0.403 (P<0.01)	0.092	—	69.89%	0.0426
		$il = b\,sl^a + c$	0.235 (P<0.01)	0.214	-0.134 (P=0.60)	69.80%	0.0428
iw	88	$iw = b\,sl^a$	0.675 (P<0.01)	0.139	—	93.05%	0.1698
		$iw = b\,sl^a + c$	0.305 (P<0.01)	0.633	-0.597 (P<0.01)	95.40%	0.0937
pl	67	$pl = b\,sl^a$	1.381 (P<0.01)	0.027	—	92.28%	2.1374
		$pl = b\,sl^a + c$	0.701 (P<0.01)	0.259	-0.507 (P<0.01)	98.36%	0.2117

the iw/sl ratio due to the negative y intercept of the curve of best fit of iw on sl, this is not apparent in the observed values of the corresponding ratio (Fig. 2.5C).

Overall morphology of the internal ligament and contained lithodesma gradually shift to a laterally elongated shape in larger specimens (Fig. 2.6), a tendency reflected by the steeper slope of the iw against sl curves relative to il against sl (Fig. 2.5A). This modification in shape is probably a consequence of spatial conflict with the developing nymphs of the parivincular ligament, which contact the posterior border of the lithodesma and, consequently, limit growth of the internal ligament in a posterior direction (Figs 2.2J, K, L).

The parivincular ligament grows in length at a faster rate than the valves following its relatively late ontogenetic appearance (Figs 2.5B, D). This results in a steep increase of the pl/sl ratio in between approximately 2.5 and 7.5 mm in shell length. The pl/sl ratio of 8% attained by the end of this interval is subsequently maintained throughout the observed range of sizes (Fig. 2.5D).

2.3.2 Previous Models of Ligament Structure in *Thracia*

Several morphological descriptions of the hinge of *Thracia* are available and it has been long established that the ligament of adult specimens may comprise both external and internal parts (e.g. Forbes & Hanley, 1853; Reeve, 1859). However, with observations of larval and early juvenile stages lacking, few authors have attempted to explain the origin and relationships between these parts.

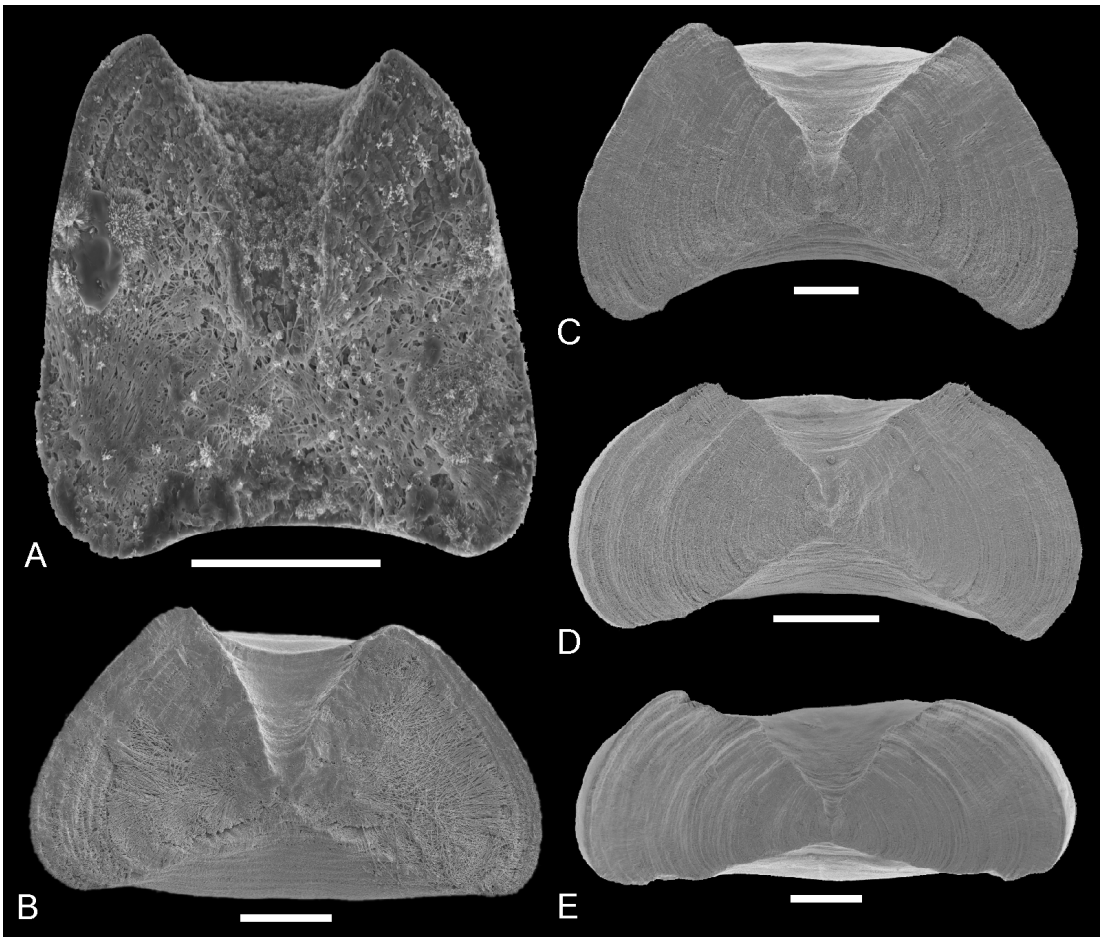


Figure 2.6: *T. phaseolina*. Dorsal view of the lithodesma of a growth series, showing the gradual shift in morphology from a quadrangular, antero-posteriorly elongated shape in early juveniles (**A**) to a wide semi-circular arch, compressed antero-posteriorly (**E**). All specimens treated in commercial bleach and figured with the anterior end of the lithodesma toward the top of the page. Length of the shell: **A** = 1.34 mm; **B** = 2.42 mm; **C** = 3.44 mm; **D** = 5.56 mm; **E** = 9.11 mm. Scale bars: **A** to **C** = 40 μm; **D** and **E** = 100 μm

Allen (1961*a*) studied the shell and hinge of British species of *Thracia* (including *T. phaseolina*) and was probably the first author to clearly express his views on the identity of each portion of the ligamental apparatus. According to his scheme, the ligament comprises a single fibrous layer in between two lamellar layers, and the lithodesma is a component of the anterior lamellar layer (Allen, 1961*a*, fig. 2).

In a comprehensive study of ligament structure in anomalodesmatans, Yonge & Morton (1980) analysed *T. phaseolina* and concluded that the lithodesma is formed by calcification of the anterior end of the fibrous layer, not of the lamellar layer as had been proposed by Allen (1961*a*). Yonge & Morton (1980, fig. 15) depicted the ligament

of the species as comprising one fibrous and one lamellar layer only (inner and outer layers of the terminology then in use).

The lithodesma of *T. phaseolina* is indeed part of a fibrous layer, but this layer is not joined with the fibrous portion of the parivincular ligament, as envisaged by Yonge & Morton (1980). Instead, the complex morphology of the ligament of *Thracia* is better regarded as a result of discontinuous development of fibrous ligament, as explained below.

2.3.3 Discontinuous Ligament Ontogeny

In the early ontogeny of all bivalved molluscs, the first fibrous ligament to form (F1) is invariably internal (Bernard, 1895) and may occupy the anterior, central or posterior portion of the hinge (Waller, 1990; Malchus, 2004). In lucinids, venerids and several other taxa, the adult ligament appears to be simply a continuation of F1, which commonly migrates to an external position during ontogeny (Le Pennec, 1973; LaBarbera, 1974; Lutz *et al.*, 1982; Goodsell *et al.*, 1992).

Alternatively, an independent, separate layer of fibrous ligament (F2) may emerge during early postlarval morphogenesis. In these cases, F1 is either abandoned and absorbed by the animal, or both fibrous layers remain active throughout life. This type of development, characterised by discontinuous ontogeny of fibrous ligament, is typical of pteriomorphians (Waller, 1998; Malchus, 2004) but may also take place in several palaeoheterodont (Le Pennec & Jüngbluth, 1983) and heterodont taxa (Trueman, 1966; Malchus, 2005).

Development of the ligament of *T. phaseolina* conforms to the latter, discontinuous model, evidenced by the emergence of the fibrous layer of the parivincular ligament as an independent subunit, separated some 15 μm from the internal ligament, and the distinct rates and directions of growth exhibited by the two ligaments. I interpret the position of the origination point of the internal ligament, in the posterior half of the prodissoconch hinge line, as circumstantial evidence that this fibrous layer represents F1, pending knowledge of larval and early postlarval stages. The fibrous layer of the parivincular ligament would then correspond to F2. Although I did not have suitable material to determine the shell length at which the internal ligament becomes visible, if it forms in preparation for or just after metamorphosis as is general in bivalves (Waller, 1990), then the length of the larval shell will provide a close approximation. Ockelmann (1965, Fig. 3-1) illustrated a larval shell of *T. phaseolina* measuring approximately 235

μm in length, and I have similarly determined a mean length of 214 μm ± 11 SD from SEM images of four individuals.

2.3.4 Functional Morphology of F1 and Associated Lithodesma

Even though the occurrence and taxonomic value of the lithodesma in representatives of *Thracia* have been debated since the early 19th Century (e.g. Scacchi, 1836; Deshayes, 1845–1848; Dall, 1903; Allen, 1961*a*; Coan, 1990*b*), little attention has been paid to its function, apart from a brief discussion by Yonge & Morton (1980).

Yonge (1976, 1978) investigated the functional morphology of the ligamental apparatus of lyonsiids and concluded that the lithodesma prevents a ventrally displaced, widened ligament from bending ventrally when the adductors contract. Yonge & Morton (1980, p. 264) extended this hypothesis to all but three anomalodesmatan families (Thraciidae, Periplomatidae and Laternulidae) in which conditions were deemed "totally different", because the "ligament is *not* ventrally displaced" and the lithodesma "solely concerned with alignment of the valves".

However, Yonge & Morton's (1980) interpretation of the ligament of *Thracia* seems to be exclusively based on examination of large specimens, in which F1 and its lithodesma are either very small when compared to the rest of the ligamental apparatus or completely absent (Coan, 1990*b*; Sartori & Domaneschi, 2005). As shown herein, in specimens of *T. phaseolina* smaller than ∼2.5 mm, F1 alone is responsible for forcing the valves to gape upon relaxation of the adductor muscles. Calcification of its mid sector into a solid lithodesma ensures an appropriate width to cross sectional area ratio of its resilient left and right portions, minimising the risk of bending and being ruptured by tensional stress. Hence, the structure and mode of operation of F1 and its lithodesma is identical to that of lyonsiids and other anomalodesmatans, but in *T. phaseolina* responsibility for opening the shell is gradually transferred to F2 by the differential growth of these ligamental components.

2.4 Comparative morphology of the ligament in extant anomalodesmatans

In most comparative studies, observations are organised either taxonomically or beginning with the simplest and progressing toward more complex structures. For the purposes of this discussion I have found it convenient, however, to begin with taxa traditionally classed under Thracioidea, some of which have been described as bearing

"one of the most complex ligaments found among the bivalves" (Savazzi, 1990, p. 93), for two main reasons.

First, Thracioidea is the only anomalodesmatan nominal superfamily for which observations of the development of the ligament are currently available, albeit admittedly incomplete.

Second and more importantly, variability of ligament structure in this ensemble encompasses most adult morphologies found in Anomalodesmata as a whole, so that a detailed investigation of the organ in Thracioidea will serve well as a guide to the interpretation of ligament architecture in the other anomalodesmatan superfamilies, for which ontogenetic data is wanting.

2.4.1 Thracioidea

The thracioid hinge has been examined by several authors (e.g. Allen, 1960*a*, 1961*a*; Morton, 1976; Coan, 1990*b*; Savazzi, 1990; Kamenev & Nadtochy, 1998; Kamenev, 2002; Sartori & Domaneschi, 2005), and the wide range of ligament morphologies displayed by adults of the group traditionally described as:

- parivincular ligament (e.g. in *Thracia meridionalis*, Fig. 2.7A);
- parivincular ligament, with an anterior lithodesma (e.g. in *Thracia phaseolina*, Fig. 2.7B);
- internal ligament attached to chondrophores (e.g. in *Laternula elliptica*, Fig. 2.7C);
- internal ligament attached to chondrophores, with an anterior lithodesma (e.g. in *Periploma compressum*, Fig. 2.7D); and
- internal ligament attached to resilifers, with a central lithodesma (e.g. in *Parvithracia suteri*, Fig. 2.7E).

Throughout section 2.3 above I have shown that the ligament of *T. phaseolina* is in fact multiple, with lithodesma and parivincular ligament representing independent and disjunct layers of fibrous ligament, the former presumably continuous with the larval ligament (F1) and the latter secreted from the early juvenile phase into adulthood (F2).

Observations of less complete growth series of *T. meridionalis*, *L. elliptica* and *P. compressum* provide direct evidence that their ligaments are also disjunct. While adults of *T. meridionalis* display only a typical parivincular ligament (Fig. 2.7A), in the smallest specimens available for examination (two individuals measuring 7.5 mm in shell

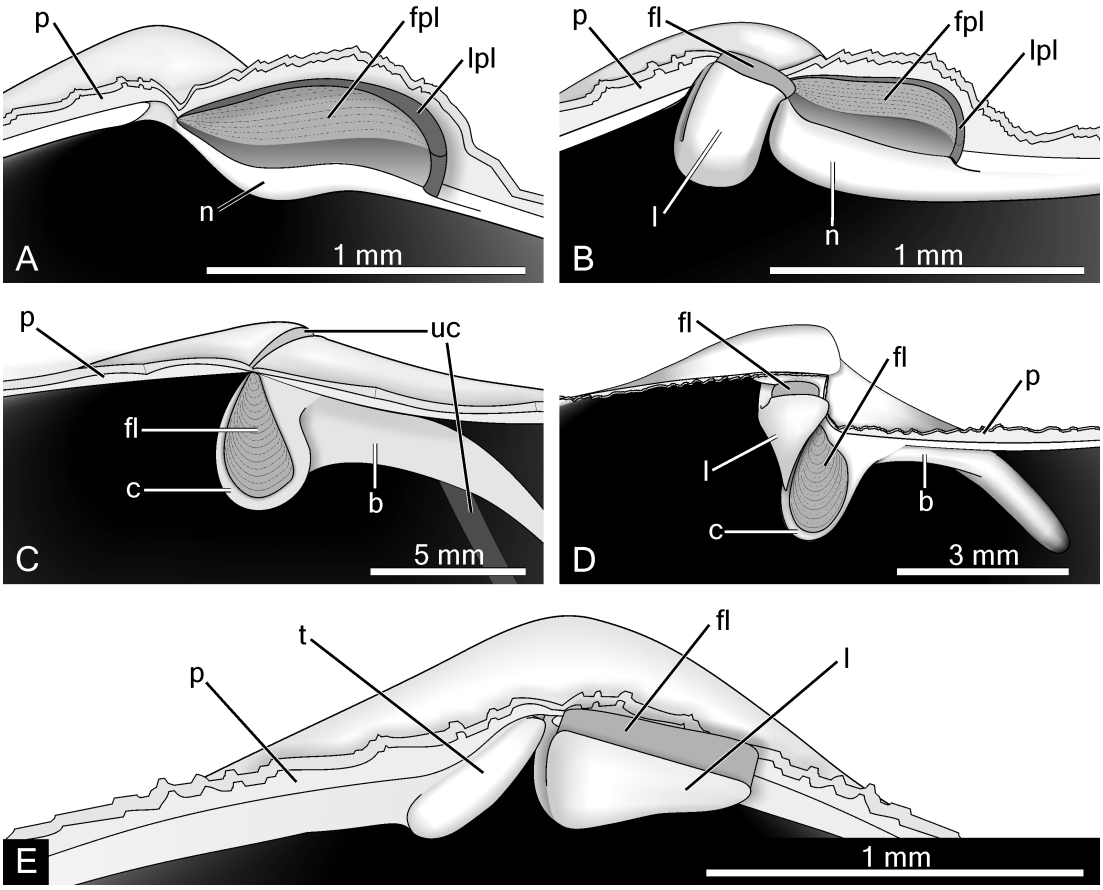


Figure 2.7: Line drawings of the hinge of the right valve of adult thracioids, showing the diversity of ligament morphologies found in the group. All in lateral view. **A**. *Thracia meridionalis*, parivincular ligament. **B**. *Thracia phaseolina*, multiple ligament comprising a dorsal (parivincular) and an internal (cardinal) fibrous layer. **C**. *Laternula elliptica*, internal ligament supported by chondrophores. **D**. *Periploma compressum*, multiple ligament comprising two internal fibrous layers, one supported by chondrophores and one calcified along its sagittal plan into a lithodesma. **E**. *Parvithracia suteri*, internal (cardinal) ligament, calcified along its sagittal plan into a lithodesma. Abbreviations: **b**, buttress; **c**, chondrophore; **fl**, fibrous layer; **fpl**, fibrous layer of the parivincular ligament; **l**, lithodesma; **lpl**, lamellar layer of the parivincular ligament; **n**, nymph; **p**, periostracum; **t**, tooth; **uc**, umbonal slit (crack).

length), the hinge comprised two ligamental components. The first is an internal layer of fibrous ligament, attached to left and right resilifers in the cardinal area, immediately under the umbones (Fig. 2.8A, E). This layer is sagittally calcified into a lithodesma and grows chiefly in a ventral direction, as evidenced by its shape and growth lines on the resilifers (Fig. 2.8E, F).

Posterior to the cardinal layer is the origination point of the parivincular ligament, the second component of the ligamental apparatus, which grows chiefly in a posterior direction and is supported by a robust nymphal ridge on each valve. As with heteroconchs in general, the bulk of the parivincular ligament is fibrous, with thin sheets of lamellar ligament and periostracum overlaying the structure.

The fibrous layers of the cardinal and parivincular components are discontinuous but very close to each other, their attachment areas being separated by only a few micrometers (Fig. 2.8F). Hence, at this stage the ligament of *T. meridionalis* is multiple and identical in configuration to that of juvenile and adult *T. phaseolina*. By analogy with that species, the internal, cardinal fibrous layer and contained lithodesma is interpreted as the first ligament to form (F1) and the parivincular ligament as the second (F2) although the sequence of appearance was not observed in *T. meridionalis*.

Larger specimens of *T. meridionalis* evidence reworking of the hinge region, with gradual absorption of F1 and associated resilifers. Curiously, concomitant to reduction and eventual disappearance of F1, a pit of unknown function is carved into the anterior end of both nymphal ridges (Fig. 2.8B–D, F–J). The pit is devoid of ligamental fabric and, in material with the soft parts preserved, was always found occupied by an evagination of the mantle isthmus. The ligamental apparatus of adult specimens has F2 as its sole fibrous layer and, importantly, bears no cue of the former presence of a cardinal fibrous ligament layer (Fig. 2.8D, I–J).

Adult periplomatids and laternulids have a completely internal primary ligamental apparatus (a "secondary ligament" formed by the dorsal periostracum is obviously external, as in other bivalves). The ligament is supported by large chondrophores projecting ventrally from the dorsal margin of each valve and an anterior, V-shaped lithodesma is usually present (Fig. 2.7C, D).

Two early juveniles of *P. compressum* (1.24 and 2.31 mm in shell length) revealed an internal, fibrous layer as the sole resilient component of their hinge (Fig. 2.9A). This layer bears a lithodesma along its sagittal sector and has its anterior end positioned immediately under the beaks, from where it appears to expand chiefly postero-ventrally.

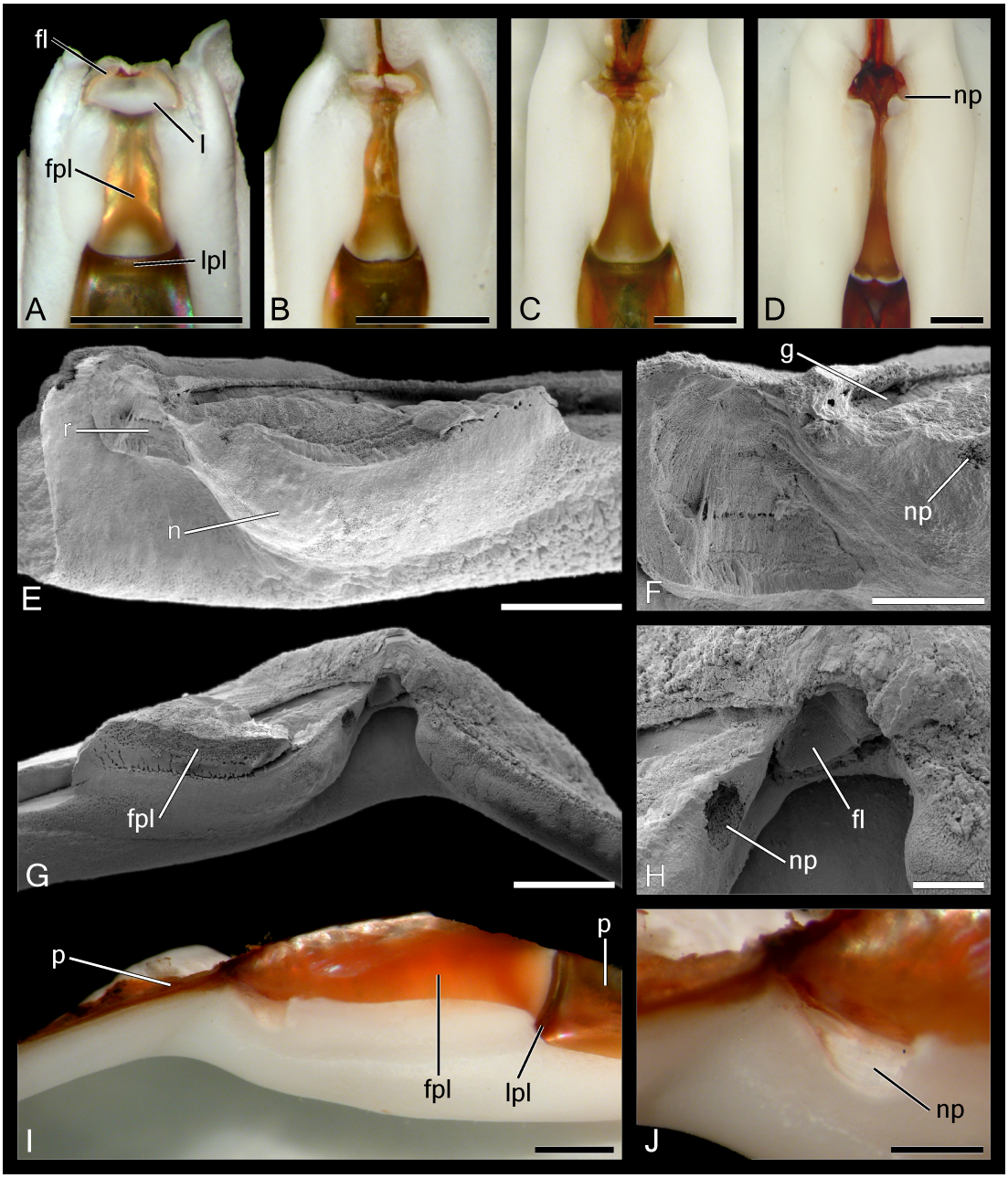


Figure 2.8: *Thracia meridionalis*. Ventral (**A** to **D**) and lateral (**E** to **J**) views of the hinge of a growth series, showing gradual absorption of F1 and its resilifers, with concomitant development of a pit at the anterior end of the nymphs. Anterior end towards the top in **A** to **D**. Specimens **E** to **H** were bleached for five minutes prior to preparation for SEM. **F**, **H** and **J** are details of the cardinal area of **E**, **G** and **I**, respectively. **E**, **F**, **I** and **J**. Right valve. **G** and **H**. Left valve. Abbreviations: **fl**, fibrous layer; **fpl**, fibrous layer of parivincular ligament; **g**, attachment groove of lamellar layer; **l**, lithodesma; **lpl**, lamellar layer of parivincular ligament; **n**, nymph; **np**, nymphal pit; **p**, periostracum; **r**, resilifer. Length of the shell: **A**, **E** and **F** = 7.5 mm; **B**, **G** and **H** = 11 mm; **C** = 19.16 mm; **D** = 28.94 mm; **I** and **J** = 27.68 mm. Scale bars: **A** to **D** = 1 mm; **E** = 200 μm; **F** = 80 μm; **G** = 400 μm; **H** = 100 μm; **I** = 1 mm; **J** = 500 μm.

It most probably represents a continuation of the larval ligament and is thus provisionally identified as F1, pending knowledge of larval and earlier post-larval developmental stages.

The smallest specimen of *P. compressum* found with chondrophores measured 1.82 mm in shell length and had already developed small umbonal slits radiating from the beaks immediately in front of F1 and its resilifers (Fig. 2.9B). The chondrophores form as two ventrally-projecting bosses just posterior to F1 (Fig. 2.9B) and are bridged by an additional fibrous ligament layer (F2) which is discontinuous with F1, despite their close proximity.

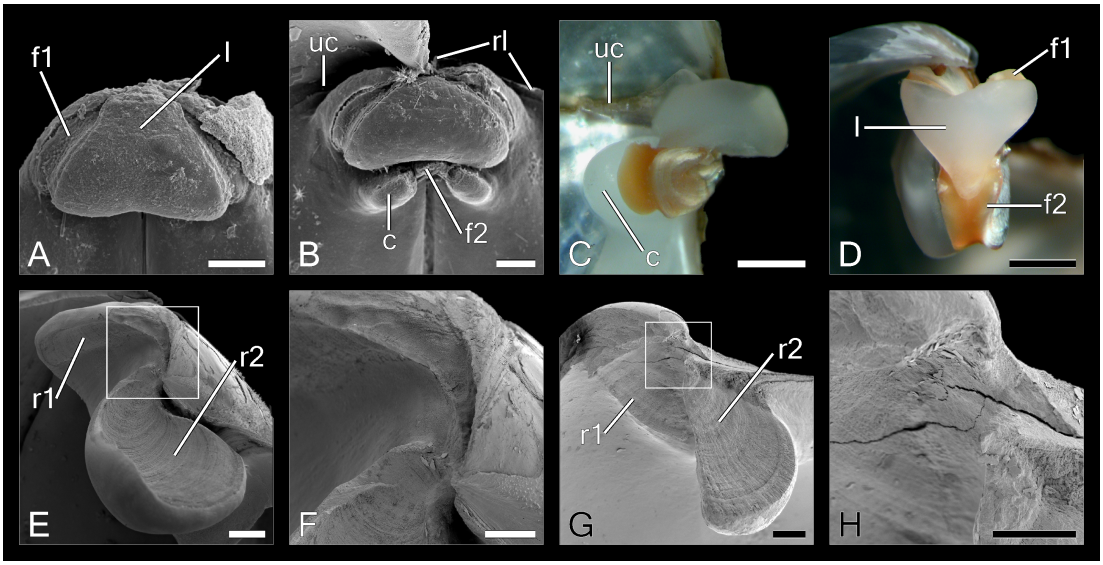


Figure 2.9: **A** to **D**. Hinge of *Periploma compressum* in ventral (**A** to **C**; anterior end towards the top) and anterior (**D**) views. **A**. Ligament of an early juvenile (shell length = 2.31 mm; MZSP 44061), comprising only a fibrous layer with sagittal lithodesma. **B** to **D**. Early juvenile (**B**; shell length = 1.82 mm; MZSP 44065) and adult (**C** and **D**; shell length = 33.96 mm; CENEMAR, unregistered) showing a multiple ligament comprising a cardinal fibrous layer with sagittal lithodesma and a posterior fibrous layer supported by chondrophores. Notice that the latter layer is much smaller than the former in the early juvenile, but the inverse relationship occurs at the adult stage. **E** to **H**. Scanning electron micrographs of bleached, right valve hinges of adult *Laternula truncata* (**E** and **F**) and *Trigonothracia jinxingae* (**G** and **H**), showing a gap between the attachment areas of the fibrous layers. **F** and **H** are details of the areas delimited by the square in **E** and **G**, respectively. Abbreviations: **c**, chondrophore; **f1**, firstly formed postlarval fibrous layer; **f2**, secondly formed postlarval fibrous layer; **l**, lithodesma; **rl**, repair ligament that bridges anterior and posterior margins of the umbonal slit; **r1**, attachment area (resilifer) of f1; **r2**, attachment area (resilifer) of f2; **uc**, umbonal slit. Scale bars: **A** and **B** = 50 μm; **C** and **D** = 1 mm; **E** = 0.5 mm; **F** and **G** = 150 μm; **H** = 100 μm.

Ultrastructural analyses of the attachment areas of F1 and F2 in adult shells of other species displaying a multiple adult ligament of similar morphology revealed a

small but definite gap between the origination points of these fibrous layers, confirming their disjunct character (Fig. 2.9E–H).

At least in *P. compressum*, chondrophores and F2 grow at a much faster rate than F1 to become the main components of the adult ligament (Fig. 2.9C–D). Concomitant with the positive allometric growth of F2 and probably largely due to spacial conflicts arising from this process, F1 and its lithodesma change both shape and growth direction, becoming increasingly elongated dorso-ventrally and expanding chiefly antero-ventrally (Fig. 2.9D).

The relationships between the ligament architectures of *L. elliptica* and *P. compressum* parallels those noted above between *T. meridionalis* and *T. phaseolina*. That is, although the adult hinge of *L. elliptica* shows an internal ligament supported by chondrophores as its sole component (Fig. 2.7), analysis of juveniles reveals analogous conditions to those of *P. compressum*.

In the smallest juvenile of *L. elliptica* available for examination (5.46 mm in shell length), the ligament is multiple, with two independent fibrous layers. From the anterior to the posterior end of the hinge, the first fibrous layer is sagitally calcified into a lithodesma and the second supported by one small chondrophore in each valve (Fig. 2.10A). These fibrous layers are tentatively identified as F1 (bearing a lithodesma) and F2 (supported by chondrophores) by analogy with the ligament of *P. compressum*, although their order of appearance was not observed. Whereas in the smallest analysed *L. elliptica* F1 was the most conspicuous ligament layer, with the width of its lithodesma representing approximately 5.8% of total shell lengh, a trend toward relative reduction of this layer was verified in larger individuals. Thus, in specimens measuring 7.56, 10.08 and 12.28 mm in shell length, the relative width of the lithodesma decreased to approximately 5.0, 4.3 and 3.0% of total shell length, respectively (Fig. 2.10B–E). In a specimen measuring 22.8 mm in shell length, F1, its lithodesma and attachment areas had been completely absorbed (Fig. 2.10F) and, similarly to *T. meridionalis*, adult specimens of *L. elliptica* bear no hints of the former presence of an additional ligament layer.

Despite the obvious differences between the chondrophores of periplomatids and laternulids and the typical nymphs of the species of *Thracia* discussed above, I concur with previous authors (e.g. Yonge & Morton, 1980) in regarding them as homologues because a graded morphological series exist which bridges the gap between these organs. An example of a somewhat intermediate stage between the two types of support struc-

Figure 2.10: *Laternula elliptica*. Ventral view of the hinge of a growth series, showing gradual absorption of F1 and its attachment areas. Anterior end towards the top. Micrograph **E** is a detail of the area delimited by the square in **D**. Abbreviations: **c**, chondrophore; **fl**, fibrous layer; **l**, lithodesma; **p**, periostracum; **pro**, anterior projection of chondrophore, bearing resilifer of F1; **uc**, umbonal slit. Length of the shell: **A** = 5.46 mm; **B** = 7.56 mm; **C** = 10.08 mm; **D** and **E** = 12.28 mm; **F** = 22.78 mm. Scale bars: **A** to **E** = 200 μm; **F** = 1 mm.

tures is found in *Thracia similis*, whose parivincular ligament is short antero-posteriorly with a rounded nymph that projects well below the dorsal shell margin (Fig. 2.11).

Finally, adults of a number of genera currently referred to the probably polyphyletic family Thraciidae (see Dreyer *et al.*, 2003; Harper *et al.*, 2006), including *Asthenothaerus*, *Bushia*, *Lampeia*, *Parvithracia*, and *Thraciopsis*, bear an internal ligament with central lithodesma as the sole component of their hinge. None of the representatives of these genera surveyed herein showed any trace of a multiple ligament, nor any was found in literature descriptions (e.g. Coan, 1990*b*; Kamenev & Nadtochy, 1998; Kamenev, 2002; Marshall, 2002). Early post-larval stages were, however, not available for the present study.

The ligament of these forms invariably originates immediately under the umbones, grows postero-ventrally and attach to resilifers that are flush with or project little from either the hinge plate or the internal surface of the shell walls (Fig. 2.12). Nymphal

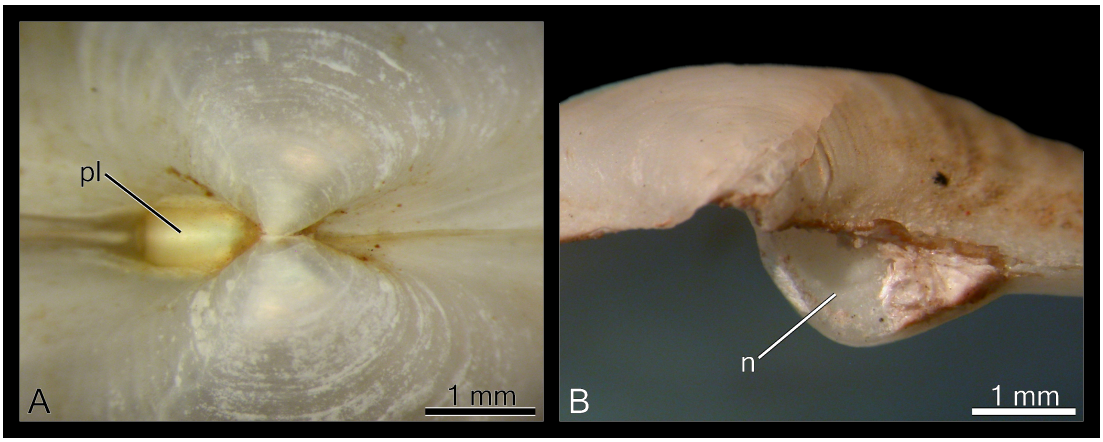


Figure 2.11: *Thracia similis*. **A**. Dorsal view of the umbonal region, showing the external, parivincular ligament (MZSP 19.986). **B**. Lateral view of the hinge of a right valve (MZSP 19.972), showing a rounded nymph that projects well below the dorsal shell margin. Abbreviations: **n**, nymph; **pl**, parivincular ligament.

ridges, chondrophores or other projecting support structures are lacking. The lithodesma is always present and similar in shape to those of early juvenile *Thracia*, *Periploma* and *Laternula*. Hence, this ligament is in every aspect similar to F1 of other thracioids and the homology between these structures is tentatively suggested.

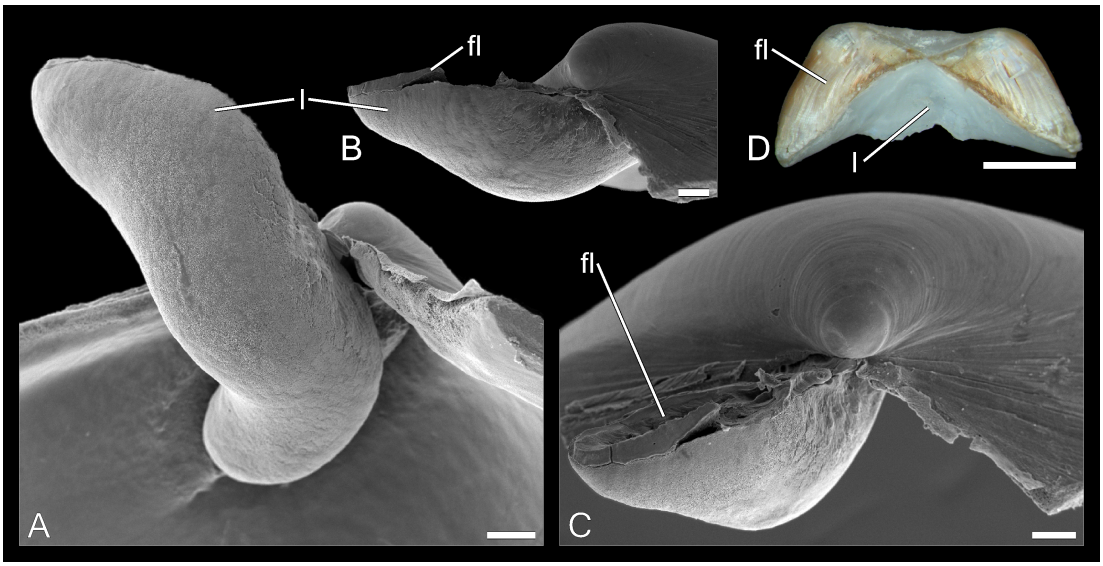


Figure 2.12: **A** to **C**. Hinge of the left valve of *Parvithracia fragilissima* in latero-ventral, anterior and antero-lateral views, respectively (NMNZ M. 155144). **D**. Dorsal view of the ligament of *Asthenothaerus maxwelli*, detached from the shell. Anterior end towards the top (NMNZ M. 183057). Abbreviations: **fl**, fibrous ligament; **l**, lithodesma. Scale bars: **A** to **C** = 100 μm; **D** = 2 mm.

2.4.2 Pholadomyoidea

Virtually all recent descriptions and diagnoses of pholadomyoids report a parivincular ligament as the sole resilient component of the hinge (e.g. Morton, 1980, 1982, 1985*a*; Boss, 1982; Prezant, 1998*c*, but see Krylova 2006). However, up to the 1970s the possible occurrence of an additional, internal ligament unit was the focus of much debate.

As noted in more detail in section 6.1.4, the taxonomic composition of Pholadomyoidea is not universally agreed upon and the Palaeozoic families Edmondiidae and Megadesmidae are at times classed here (e.g. by Runnegar, 1974), and at others referred to a separate superfamily (e.g. by Morris *et al.*, 1991).

Edmondiids are diagnosed by an internal, narrow plate, partly covered by the umbo and positioned underneath the dorsal shell margin (Waterhouse, 1966, pls 15–17; Runnegar & Newell, 1974, figs 2, 5). In establishing the type genus of the family, de Koninck (1844, p. 66) noted that this plate probably supported an internal ligament and considered that the organisation of the hinge of *Edmondia*, the prominence of its umbones and the morphology of the lunule made the presence of two ligaments in the genus very probable. For many decades to follow, the possible role of the plates as attachment areas for an internal ligament was discussed by a number of authors (e.g. Waterhouse, 1966; Runnegar, 1967; Astafieva-Urbaitis, 1970, 1973) but its function remained nevertheless unproven.

In many ways, the work of Waterhouse (1966, 1969*a*,*b*) represented the pinnacle of the hypothesis of a multiple ligament in pholadomyoids. Firstly because Waterhouse was convinced not only that a depression associated with the edmondiid plates indeed supported an internal ligament, as suggested by previous authors, but also that an homologous structure with identical function occurred in several megadesmids and pholadomyids, including the type species of Pholadomyoidea, the extant *Pholadomya candida*. To Waterhouse (1969*a*, p. 99) this inner depression along the hinge, with an internal ligament, represented "one of the chief characteristics in many members of the bivalve superfamily Pholadomyacea". And secondly because Waterhouse's work was closely followed by the influential papers of Runnegar (1972) and Runnegar & Newell (1974), which led to abandonment of the disputed hypothesis of an internal ligament in the group.

Runnegar (1972, p. 48) studied *P. candida* and was emphatic in asserting that the "depression in the hinge plate of each valve which Waterhouse (1969, p. 104) interpreted

as a ligament pit (resilium) has some other function, as specimens with otherwise intact ligaments (Plate 1j; Waterhouse, 1969, fig. 1b) have no trace of ligamental material in this depression".

Runnegar & Newell (1974, p. 1,2) reported on silicified hinges of edmondiids and concluded that the internal plate "contains a row of small suspensory muscle insertions, previously interpreted as a ligament groove" and hence "is not, as Waterhouse (1969b) and others have suggested, the site of an internal ligament".

After examining the hinge of several adult *P. candida*, I cannot agree with Runnegar (1972) because most specimens with a relatively complete parivincular ligament also exhibit clear evidence of ligamental material in a depression immediately under the umbones and anterior to the nymphs (Fig. 2.13A–F). Waller (1990, p. 56) similarly observed ligamental material in this pit, which he interpreted as repair ligament. However, the occurrence in at least some specimens of a clearly differentiated attachment area (resilifer, Fig. 2.13E, F) for this material indicates it is not repair ligament, which, as Waller (1990) remarks, is never associated with a defined fossette but forms irregularly wherever and whenever the need for repair arises. Instead, the association of this ligament with a resilifer in the cardinal area, as well as a comparison of its colour with that of the distinct layers of the parivincular ligament, suggest a fibrous composition.

This presumably fibrous, internal ligament component display a chiefly ventral growth direction and in some specimens appear discontinuous with the parivincular ligament (Fig. 2.13B). These observations suggest the ligament of *P. candida* is multiple, with independent cardinal and parivincular fibrous ligament layers which are, nevertheless, very near to one another, and may appear joined due to secretion of repair material along their borders (Fig. 2.13F).

Finally, the general morphology of the hinge plate of *P. candida* is rather variable, particularly in the development of the anterior tooth-like projection and umbonal pit (compare, for instance, Figures 2.13A, C with Runnegar, 1972, pl. 1j–l and Morton, 1980, pl. 3). This is suggestive of extensive reworking of the cardinal area, probably involving absorption of the internal ligament layer, which could account for the varying degrees of expression of this component among individuals and the polar opinions held by previous authors regarding its existence and significance.

Conditions in the other extant pholadomyoid family, Parilimyidae, appear compatible with the above interpretation. In *Parilimya neozelanica* the adult ligament is clearly multiple, comprising two separate fibrous layers (Fig. 2.13G–I). From the anterior to the posterior end of the hinge, the first layer is positioned in the cardinal area,

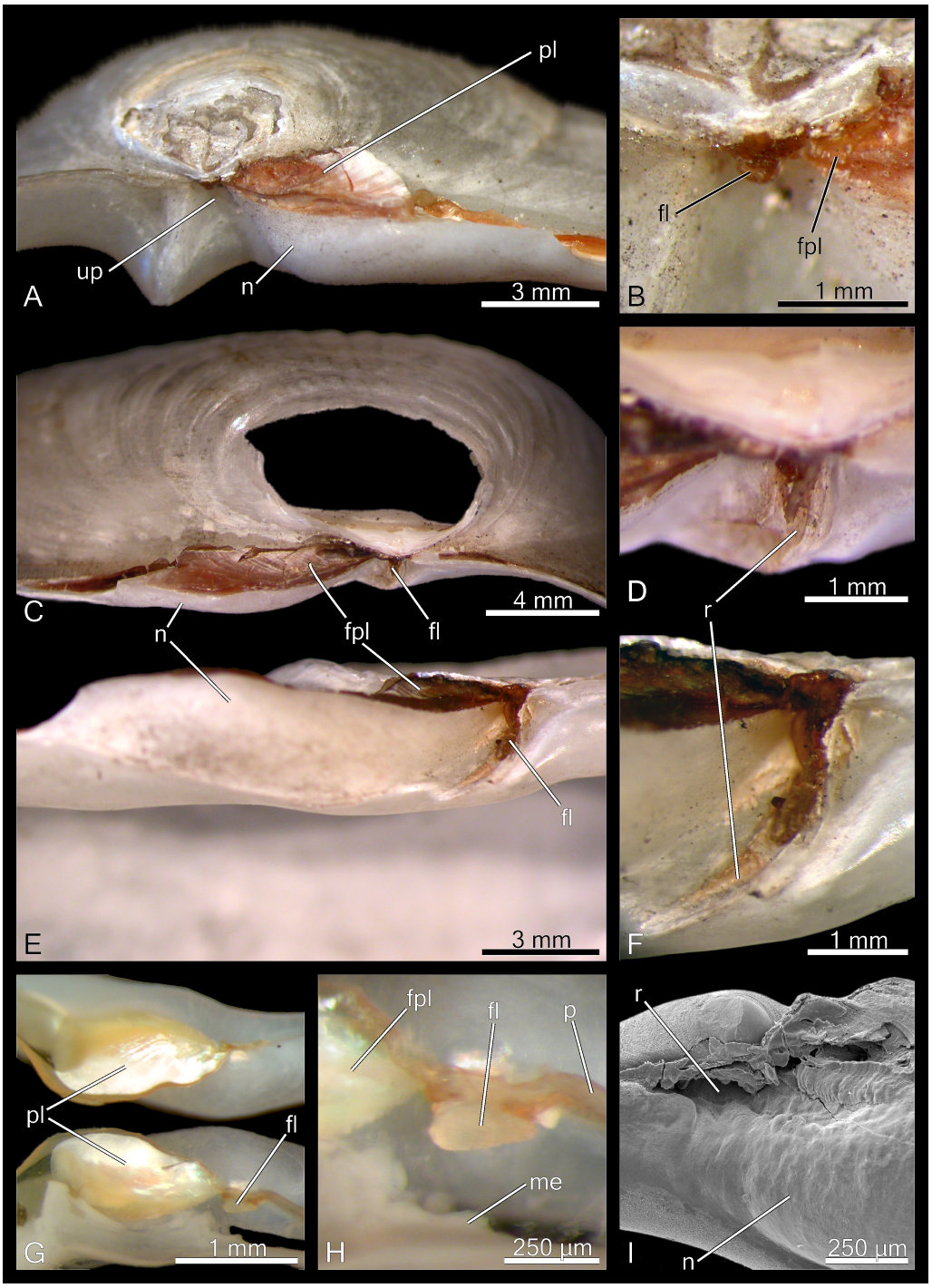


Figure 2.13: Ligament structure in extant pholadomyoids. **A** to **F**. *Pholadomya candida*. Lateral (**A** to **D**) and ventral (**E** and **F**) views of the hinge. **B**, **D** and **F** are details of the cardinal area of **A**, **C** and **E**, respectively. **A** and **B**. Right valve. ZMUC, unregistered (Tortola; shell length = 105.96 mm). **C** to **F**. Left valve. ZMUC, unregistered (St. Thomas; shell length = 92.16 mm). **G** to **I**. *Parilimya neozelanica*. NMNZ, M.183055.2004030; shell length = 16.94 mm. **G**. Lateral view of the hinge of the right (top) and left (bottom) valves. **H** and **I**. Detail of the cardinal area of the left and right valves, respectively. Abbreviations: **fl**, fibrous layer; **fpl**, fibrous layer of the parivincular ligament; **me**, epithelium of the mantle isthmus; **n**, nymph; **p**, periostracum; **pl**, parivincular ligament; **r**, resilifer; **up**, umbonal pit.

in a low pit immediately under the beaks whereas the second fibrous layer is part of a typical parivincular ligament, being hence supported by nymphs and overlaid by a thin lamellar layer. Distinct grow directions (chiefly ventral in the cardinal and posterior in the parivincular ligaments) and a clear gap between the origination points of the fibrous layers evidence that these represent independent units. Although most literature accounts of the hinge of parilimyids note only a parivincular ligament, Krylova (2006) described and illustrated a multiple ligament in two Atlantic species of *Parilimya* which matches closely the description given above.

Taken collectively, these observations suggest that in both extant pholadomyoid families the adult ligament is disjunct. Based on topological correspondence with the multiple ligament of *Thracia* and because in all bivalves the first ligament to form is secreted along the hinge line of the prodissoconch, I take the internal fibrous layer positioned in the cardinal area, immediately under the beaks, to represent F1 and the parivincular ligament F2, pending knowledge of larval and early postlarval stages.

However, unlike thracioids, a lithodesma is lacking in the cardinal ligament (F1) of all pholadomyoid specimens available for examination. This may be due to the distinct configuration of the hinge plate in the two superfamilies. In Thracioids the hinge plate is very reduced and the resilifers of the cardinal ligament nearly flush with the internal surface of the valves. Under these circumstances, calcification of the sagittal sector of F1 ensures an appropriate ratio of width to cross-sectional area of its resilient portions as the valves are gradually splayed apart by accretionary growth at the shell margin (as explained in more detail in section 2.3.4, above). Conversely, the cardinal portion of the hinge plate of *Parilimya* and *Pholadomya* protrudes ventrally and form raised attachment platforms for F1 (compare Fig. 2.13C, E with 2.12A) which effectively restrict its width as the valves grow, obviating sagittal calcification of this ligament layer.

2.4.3 Clavagelloidea

Ligament structure in clavagelloids is presently unclear. Until recently, the entire superfamily was diagnosed as having an external ligament (e.g. by Smith, 1962*b*; Keen & Smith, 1969; Smith, 1971; Morton, 1981*b*), with some authors identifying nymphs as its support structures (e.g. Dall, 1913; Boss, 1982). However, descriptions of an internal ligament in some clavagelloids are found as early as Smith (1885, 1910), and recent detailed anatomical work by Morton (1984*a*,*b*, 2002*a*, 2003*a*, 2005, 2006*a*,*b*) similarly suggests some variety in ligament morphology within the group.

For one of the clavagelloid functional groups (Clavagellidae), in which the left valve is fused to the wall of the crypt and the right valve articulates freely, several descriptions and illustrations of the shell are available in the literature (e.g. Broderip, 1835; Owen, 1835; Reeve, 1872; Soliman, 1971; Smith, 1976) but, unfortunately, the structure of the hinge has been mostly neglected. In a series of papers, Morton (1984*a*, 2003*a*, 2005, 2006*a*) described the ligament of *Dacosta*, *Dianadema* and *Stirpulina* as internal but that of *Bryopa* as external in juveniles and absent (eroded) in adults. He later changed his views on juvenile *Bryopa* and considered all extant clavagellid genera to possess an internal ligament, devoid of lithodesma (Morton, 2006*a*, table 1; 2007, p. 30).

Part of the difficulties in interpreting ligament structure in clavagellids may be related to the drastic adaptations that attend the unusual boring habit of several species, in which the animal continuously migrate forward in spite of having its left valve cemented to the wall of the borehole. Savazzi (2000, especially fig. 7) explained how *Bryopa lata* achieve this by absorbing the posterior, umbonal region of the shell while elongating its borehole in an anterior direction. Because the ligament is normally positioned at the umbonal region, it is unclear whether the organ is also lost in this process, in which case the amorphous resilient material connecting left and right valves in these taxa (Fig. 2.14A) could be interpreted as an analogous structure. The recent finding of a species of *Bryopa* without discernible ligament in the adult (Morton, 2005) seems compatible with this idea.

In material of *Dianadema multangularis* displaying intact umbones the ligament attachment areas occupy an internal position, originating immediately under the beaks and expanding in a postero-ventral direction (Fig. 2.14B, C; Carter & Tevesz, 1978, fig. 65). Each resilifer is nearly flush with the internal surface of the shell, thus closely resembling the attachment areas described for the F1 of thracioids. Contrary to the latter group, however, there is no published evidence for the presence of a lithodesma in clavagellids (Carter & Tevesz, 1978; Morton, 2003*a*).

The second clavagelloid functional group or nominal family (Penicillidae) is characterised by having both valves fused to the walls of a tubular crypt and a generally clear morphological differentiation of their bivalved shell into two portions, the oldest often termed primary or juvenile shell, and the subsequent portion secondary shell or saddle (e.g. by Morton, 1984*b*; Harper & Morton, 2004). In adults of this ensemble the hinge is invariably concealed internally by a coat of aragonite secreted concomitantly to the crypt and, in some but not all representatives, it may be similarly covered externally

by anterior and posterior bulges of the crypt wall. These features make direct observations of ligament structure methodologically difficult, and it is hence unsurprising that studies of the organ in penicillids have only been previously undertaken in one juvenile specimen of *Humphreyia strangei* and one adult *Brechites vaginiferus* (Smith, 1910; Morton, 1984*b*, 2002*b*). Both taxa possess an opisthodetic ligament comprising a single unit that is partially calcified into a lithodesma, but the position of the organ relative to the dorsal shell margin had proved somewhat contentious. While Smith (1910, p. 24) noted "a ligament attached just below the extreme margin of the valves" in *H. strangei*, implying an internal position for the structure, Morton (1984*b*) interpreted both the ligament of juvenile *H. strangei* and that of adult *B. vaginiferus* as external and, in a later generalisation, extrapolated this observation to every extant penicillid genus (Morton, 2006*b*, table 1).

Re-examination of the juvenile specimen of *H. strangei* revealed that the attachment areas of the ligament are internal and only slightly raised from the surface of the valves (Fig. 2.14D, E). They originate under the beaks and project in a postero-ventral direction, thus resembling in every aspect the resilifers of the clavagellid *D. multangularis*, described above (compare Figures 2.14B, C with D, E). Very little ligamental material remains attached to the resilifers of this individual of *H. strangei* and the lithodesma of the species, described by Smith (1910) and Morton (1984*b*), could not be located and appears to have been lost.

Examination of adult *B. vaginiferus* similarly suggests an internal position for the ligament. Figure 2.14G–I illustrates a transverse section through the crypt and posterior margin of the juvenile valves of *B. vaginiferus*, in which the configuration of the ligament and its relationship to the valves can be seen. A sudden shift in the microstructure of the bivalved shell and ligament marks the transition between the primary and secondary portions of the juvenile shell. The valves change from nacreous in the inner layer of the primary to vertical stacks of platy crystals in the secondary portion, the latter resembling the fabric of the crypt wall but with smaller and loosely organised stacks. A corresponding change takes place in the lithodesma, marked by a shift from a microstructure of tiny crystals without any obvious organisation to vertical stacks similar to those of the secondary shell. Finally, left and right resilient components of the ligament, in between the valves and the lithodesma also change considerably, from typical fibrous ligament linked to the primary shell, to a less distinct, possibly further calcified fabric attached to the secondary shell. Partial calcification of the lateral re-

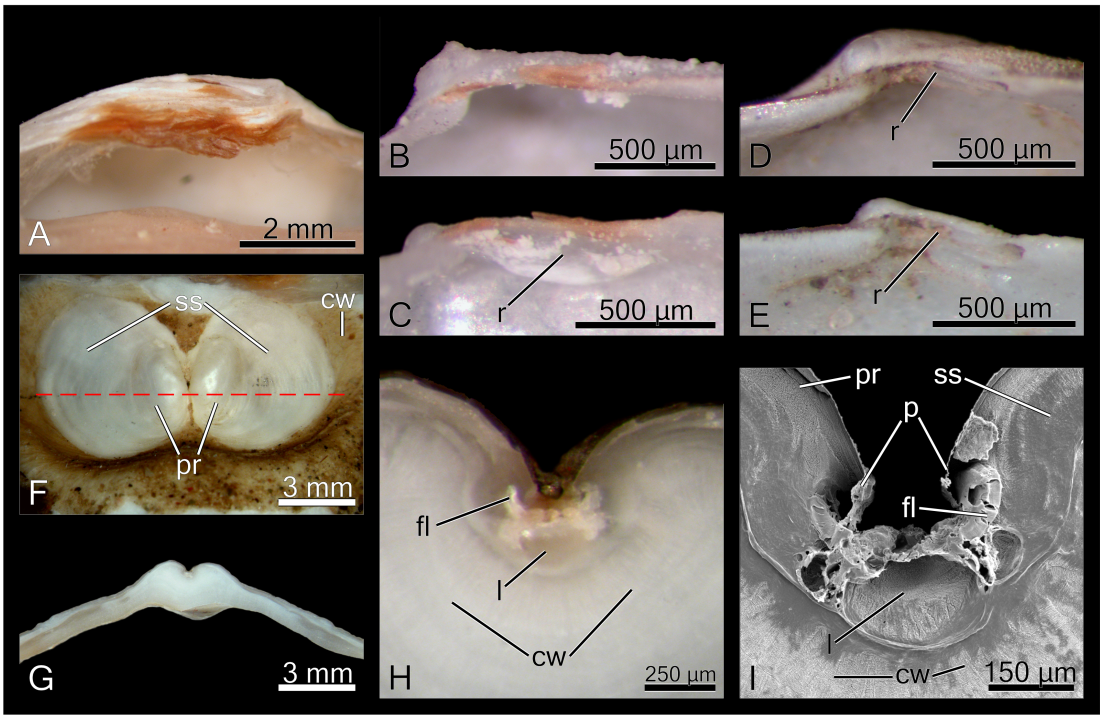


Figure 2.14: **A**. *Bryopa aperta*, BMNH unregistered. Lateral view of the hinge of the right valve, showing the resilient material that connects the valves. **B** and **C**. *Dianadema multangularis*, BMNH 1890.3.24.185–191. Lateral and ventral views of the hinge of the right valve, respectively, showing the position and morphology of the resilifer. **D** and **E**. *Humphreyia strangei*, BMNH 1910.12.31.1. Lateral and ventral views of the hinge of the right valve, respectively, showing the position and morphology of the resilifer. **F** to **I**. *Brechites vaginiferus*. **F**. External view of the juvenile shell, splayed and fused to the wall of the crypt. Anterior end towards the bottom. **G**. Transverse section through the crypt, cut along the dashed line in **F**. Dorsum towards the top. **H** and **I**. Light and electron micrographs of the commissural area of **G**, showing the ligament of the juvenile shell. Abbreviations: **cw**, wall of the crypt; **fl**, fibrous ligament; **l**, lithodesma; **p**, periostracum; **pr**, primary shell; **r**, resilifer; **ss**, secondary shell.

silient components of the ligament may represent a first step towards immobilisation of the valves, which is subsequently completed by secretion of the crypt.

Splaying of juvenile valves in penicillids complicate assessment of the position of the ligament because, if left and right juvenile valves shown in Figure 2.14F–I had their ventral margins appressed against one another, i.e. in the typical position of most bivalves, then the attachment areas of the organ would point dorsally as in a typical external ligament (e.g. nymphs of a parivincular ligament). However, the ligament of *B. vaginiferus* has its inner face convex and is in this aspect similar to internal ligaments. Most external ligaments, particularly in anomalodesmatans and other heteroconchs, form a distinct arch over the dorsal margins of the valves, being hence convex on their outer

face. Moreover and more importantly, although the earliest portions of the primary shell seems to be absent in SEM micrographs of the figured specimen (possibly due to erosion during grinding, polishing and acid etching of the material), light micrographs suggest that they extended up to the periostracal sheet shown in Figure 2.14I, so that at least initially (presumably prior to splaying of the valves and secretion of the secondary shell), the ligament was connected in an unambiguously internal position. It is probably significant in this respect that the only anomalodesmatan fibrous ligament units currently known to bear a mid-sagittal sector completely calcified into a lithodesma are invariably internal.

On the basis of the close correspondence between the topology and morphology of the resilifers of penicillids with those of the clavagellid *D. multangularis* on the one hand, and with the firstly formed fibrous layer (F1) of thracioids on the other, I tentatively suggest homology of these organs in spite of the apparent absence of a lithodesma in clavagellids.

The distinct morphology of the ligament in boring clavagellids deserves further investigation as the tenuous evidence which is currently available suggests it might be a secondary structure secreted after the erosion of the primary ligament. Analysis of the hinge of juvenile specimens of boring clavagellids should solve this issue. It is noteworthy in this respect that the cardinal area of juveniles of the boring *Bryopa aperta*, illustrated by Palazzi & Villari (2000, figs 127–129), appears closely similar to that of *D. multangularis*. Although the structure of the ligament was not discussed by Palazzi & Villari (2000), Villari (personal communication, 2009) regards the ligament as fully internal and the hinge and resilifers similar in structure to those illustrated in Figure 2.14B–D.

2.4.4 Pandoroidea and Septibranchia

The architecture of the adult hinge of pandoroids and septibranchs has been described and illustrated by several authors (e.g. Boss & Merrill, 1965; Knudsen, 1970; Allen & Turner, 1974; Allen & Morgan, 1981; Prezant & Carriker, 1983; Harper & Morton, 2000; Leal, 2008; Simone & Cunha, 2008) and studied comparatively and in detail by Yonge & Morton (1980).

It is clear from these accounts that the ligament in all four nominal pandoroid families (Pandoridae, Lyonsiidae, Myochamidae and Cleidothaeridae), as well as in verticordiids and cuspidariids among Septibranchia, closely resembles the ligament of

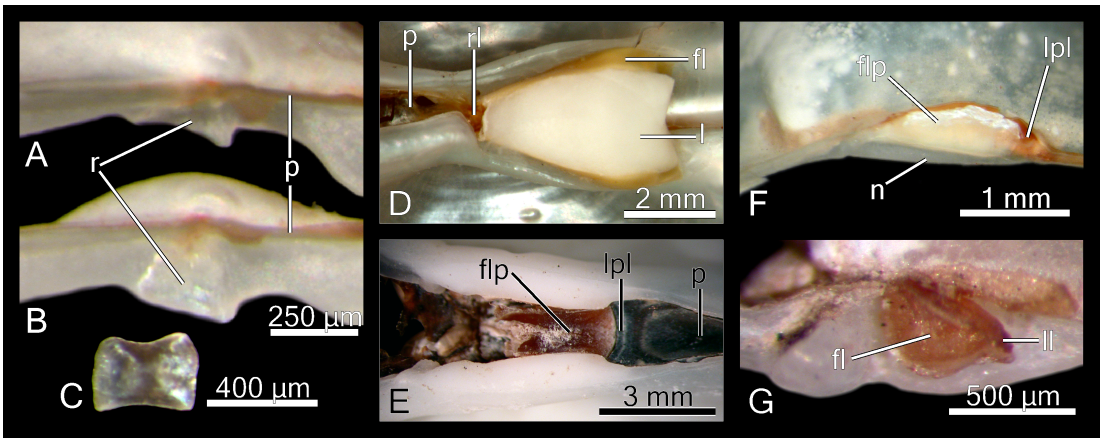


Figure 2.15: **A** to **C**. *Cardiomya cleryana*. CENEMAR, unregistered (Santos to São Francisco do Sul, Brasil; 35-62m). Shell length = 8.54 mm. **A** and **B**. Cardinal area of the hinge of the right valve in lateral and ventral views, respectively. Primary ligament removed. **C**. Dorsal view of the lithodesma. Anterior end toward the top. Left and right strips of unmodified fibrous ligament removed. **D**. *Lyonsia norwegica*. Ventral view of the hinge, showing the general structure of the ligament. BMNH, unregistered (Sarsia cruise, Stn. 360A; 13.06.1964). Shell length = 40.8 mm. **E**. *Poromya* cf *antarctica*, BMNH 20001084. Ventral view of the hinge, showing the parivincular ligament bridging right and left nymphs. Anterior end towards the left. **F**. *Poromya tornata*, MNHN, unregistered. Hinge of the right valve, showing the external, typical parivincular ligament. **G**. *Poromya granulata*, BMNH 52.1.20.37, 52.11.22.37. Hinge of the right valve, showing the internal ligament with a clear division of fibrous and lamellar layers. Abbreviations: **fl**, fibrous ligament; **flp**, fibrous layer of the parivincular ligament; **l**, lithodesma; **ll**, lamellar ligament; **lpl**, lamellar layer of the parivincular ligament; **n**, nymph; **p**, periostracum; **r**, resilifer; **rl**, repair ligament, secreted at the damaged anterior end of the ligamental apparatus.

the thracioid *Parvithracia fragilissima* and that the general description of its main features given in section 2.4.1 above applies equally well to taxa listed here.

Yonge & Morton (1980) arrived at the same general conclusion but, contrary to their opinion, I regard this type of ligament as devoid of lamellar layers and interpret the eventual formation of darker resilient material near the origination point of the fibrous layer as repair ligament secreted in response to splitting of the anterior end of the fibrous layer during growth, a common phenomenon in bivalves (see Waller, 1990). Significantly, this material is not always present and, when it does occur, appears irregularly distributed and generally associated with anterior truncation of the lithodesma (Fig. 2.15D).

Morphological variations among the different manifestations of this ligament obviously occur among pandoroids, verticordiids and cuspidariids, and these may be rather pronounced at times, especially in the development of asymmetries due to valve inequality or cementation, shape of the lithodesma, and prominence of the resilifers. The

ligament of cleidothaerids provides an extreme example of asymmetry (see Yonge & Morton, 1980, fig. 8), whereas lithodesmas may range from robust and hemi-cylindrical in some verticordiids (e.g. *Spinosipella*; see Simone & Cunha, 2008, figs 96–105) to small, elongate structures in lyonsiids and cuspidariids (Fig. 2.15C,D; see Prezant & Carriker, 1983, fig. 1), or they may be absent altogether in several pandorids and cuspidariids (Boss & Merrill, 1965; Knudsen, 1970).

Concurring with the general description given in section 2.4.1, in the vast majority of cases, attachment areas are either flush with or only slightly raised from the wall of the valves, but in some cuspidariids resilifers may project considerably from the hinge plate, forming raised, triangular platforms (Fig. 2.15A–B) which have been commonly described as chondrophores (e.g. by Bernard, 1974; Yonge & Morton, 1980). I have no objection to the use of the latter term as an informal, descriptive expression, but consider that the resilifers of cuspidariids are not homologous to the chondrophores of periplomatids and laternulids. While in the two thracioid families massive chondrophores support the putative second fibrous layer to form during ligament ontogenesis (F2), in cuspidariids the adult ligament is most probably a continuation of the larval resilium (F1). Calcification of the sagittal portion of the cuspidariid ligament into a solid lithodesma provides the most important evidence in support of this assertion. Although not an universal feature of F1 in anomalodesmatans (F1 of parilimyids, for instance, consists of typical fibrous fabric throughout), when calcification of the ligament into a rigid ossicle does occur, it seems to be restricted to this layer. Besides, even the most conspicuous cuspidariid resilifers are relatively frail when compared to the support structures associated with F2 in other anomalodesmatan groups (nymphs and chondrophores) and it seems clear from numerous descriptions and illustrations of cuspidariid hinges that a graded morphological series exists in the group, linking the projecting resilifers of some species to attachment areas that are nearly flush with the hinge plate of others (Knudsen, 1970; Poutiers & Bernard, 1995).

In the remaining septibranch family, Poromyidae, the adult ligament comprises only one couplet of fibrous and lamellar layers which varies in position from external to partially or completely internal (Poutiers & Bernard, 1995; Krylova, 2001).

Representatives with the organ in an external position display a typical parivincular ligament, with the fibrous layer supported by a nymphal ridge on each valve and the lamellar layer inserted into a groove that extends along the dorsal border of the fibrous layer to end at a fossette immediately behind the nymphs (Fig. 2.15E, F).

Poromyids in which the ligament is not visible from the outside of the shell retain a clear division between fibrous and lamellar layers, including a groove for attachment of the latter, parallel to the dorsal border of the fibrous layer. The configuration of the organ is thus similar to that of a typical parivincular ligament but instead of growing posteriorly along the dorsal margin of the shell, fibrous and lamellar layers expand in a postero-ventral direction, resulting in a fully internal ligament.

The smallest poromyid available for examination was an individual of *Poromya granulata* measuring 2.0 mm in shell length (specimens of up to 5.4 mm were present in the same lot). Neither this nor any other specimen displayed additional ligament layers in the cardinal area, or showed any signs of calcification of the ligament into a lithodesma.

Apart from cursory descriptions of a large lithodesma in *Dermatomya beringiana* by Dall (1917) and Bernard (1974), no records of additional ligament layers or a lithodesma have been made in poromyids. Leal (2008, p. 15) identified in *Dilemma* a fibrous ligament layer that is "hard and whitish, apparently in part calcified" and suggested it might represent "the remnant of a lithodesma". However, fibrous ligament is by definition partly calcified and, judging from the excellent accompanying figures (Leal, 2008, fig. 28–29), the fibrous layer of *Dilemma* appears uniform throughout, as opposed to calcified to a higher degree along its mid-sagittal sector.

Considering the presence of a well-defined layer of lamellar ligament lining the entire dorsal surface of the fibrous layer, as well as the association of this lamellar layer to a fossette just posterior to the attachment of the fibrous layer, I concur with Yonge & Morton (1980) in regarding the poromyid ligament homologous to the parivincular ligament of other anomalodesmatans, rather than to the internal ligament of cuspidariids and verticordiids. However, detailed studies of ligament structure and development in poromyids are needed to elucidate whether the adult ligament forms as a continuation of the first post-larval ligament or is disjunct as in other anomalodesmatans.

2.5 A new model for the evolution of anomalodesmatan ligament systems

In all discussions of anomalodesmatan systematics to date, the adult ligament has been tacitly considered to be simply a continuation of the larval one (Bauplan 0 of Malchus, 2004). According to such view, all manifestations of the organ are deemed homologous,

and the simplest explanation for a change in the adult position of the ligament involves its migration relative to the dorsal shell margin.

Hence, the preponderance of external ligaments in Palaeozoic anomalodesmatans, appearance of forms with subinternal and internal ligaments in the Mesozoic, and prevalent occurrence of the latter type throughout the Cenozoic were taken by Runnegar (1974, p. 905) as evidence of a gradual process of ventral displacement:

> "It seems that the totally internal ligament of shells similar to *Euciroa* [Verticordiidae] evolved from the semiinternal ligament of shells like *Ceratomya* which in turn was developed from the external ligament of shells such as *Megadesmus*. These differences provide the basis for three of the superfamilies: Pholadomyacea (external ligament), Ceratomyacea (semiinternal ligament), and Pandoracea (internal ligament)".

Boss (1978) and Yonge & Morton (1980) elaborated upon this model, describing important differences in the support structures of the ligament of the component pandoroid families, which furnished the basis for erection of Thracioidea and redefinition of Pandoroidea.

Boss (1978) noted the thracioid families Thraciidae, Periplomatidae and Laternulidae share ligaments supported by prominent structures (nymphs or chondrophores), whereas redefined Pandoroidea, comprising Lyonsiidae, Pandoridae, Myochamidae and Cleidothaeridae, is characterised by a sunken resilium that is not supported by specialised structures of the shell wall. Yonge & Morton (1980) distinguished the position of the lithodesma as anterior in Thracioidea and ventral in redefined Pandoroidea.

It is interesting to notice that Yonge & Morton (1980) discussed, albeit rather briefly, what is perhaps the most evident falsifier of the "ventral migration" model — the presence in specimens of *Thracia* of both a lithodesma and a parivincular ligament. If, as implied by the model, the former organ had its evolutionary origin in a parivincular ligament that submerged below the hinge line, then an organism could not exist which displays both the plesiomorphic and apomorphic states of this transformation series (de Pinna, 1991). Yonge & Morton (1980, p. 286) dealt with this difficulty by suggesting the ossicle of thracioids represents a "distinct structure", merely analogous to the lithodesma of other anomalodesmatans.

Another property of the prevailing model is that it strongly discourages hypotheses of iterative evolution of internal ligaments with a sagittal lithodesma ("lyonsiid" grade

of Yonge & Morton, 1980, p. 288). Bearing in mind the wide variety of different morphologies displayed by internal ligaments across the Bivalvia, it seems rather unlikely that independent events of ventral dislodgement of an external ligament converged to the same complex solution of a ligament split in the middle by a calcified ossicle (Yonge, 1976, 1978). For this reason, Yonge & Morton (1980, p. 287) found it difficult to explain the presence of a ligament of the parivincular type in poromyids, but of "lyonsiid" grade in the remaining families of Septibranchia, a group for which they believed "ideas of any polyphyletic origin can be abandoned".

Contrary to these opinions, observations gathered herein indicate that not all anomalodesmatan adult ligaments may be considered homologous. After all, some comprise a single fibrous layer which is presumably continuous with the larval ligament (F1), others a single fibrous layer that is formed subsequently (F1 is absorbed and substituted by F2), while others retain both fibrous layers into adulthood (F1 and F2 are present). Anomalodesmatan ligaments thus fall into two broad categories regarding their putative mode of development: (1) those which are simply a continuation of the larval ligament, and (2) those characterised by discontinuous ontogeny of fibrous ligament. Which of these modes of development is plesiomorphic must be considered if we are to understand the evolution of ligament systems within the group.

Both outgroup analysis and stratigraphy support the assertion that the parivincular ligament system represents the plesiomorphic state of the organ in anomalodesmatans (Waller, 1998; Morris *et al.*, 1991). Of the three extant groups with an adult parivincular ligament, direct evidence of discontinuous ontogeny was found herein for Thraciidae and Pholadomyoidea, whereas conditions in Poromyidae neither support nor reject the occurrence of this mode of development. These results suggest that discontinuous ontogeny of fibrous ligament, more likely than not, characterised the ancestor of crown-group Anomalodesmata. Hence, derivation of each type of ligament now found within the group should be sought from a primitively disjunct ligament.

An obvious issue in devising a model for ligament evolution that takes into account the mode of development of the organ is its utility. If the model is to be useful for phylogenetic inference and systematic research, it is essential that homologies may be established with some confidence based on the examination of adult specimens because, for most anomalodesmatans, this is the only life stage available in museum collections. Fortunately, a number of differences between F1 and F2 have been noticed in species displaying both layers, which may be used to distinguish which of the two is represented in taxa with a single adult fibrous layer. Fibrous layer F1 originates under the umbones,

lacks prominent support structures of the shell wall, is invariably internal and devoid of accompanying lamellar layers, and frequently has its mid-sagittal sector calcified into a solid lithodesma. Conversely, F2 may be external or internal, is always supported by either nymphs or chondrophores, devoid of lithodesma, and usually bears a lamellar layer bordering its postero-dorsal margin.

Based on the criteria above, the single fibrous layer of the adult ligaments of the thraciid genera *Asthenothaerus*, *Bushia*, *Lampeia*, *Parvithracia* and *Thraciopsis*, of all Pandoroidea and clavagelloids except boring clavagellids, and of all verticordiids and cuspidariids is considered to represent F1, whereas the adult ligament of poromyids is thought to represent F2.

The new model proposed herein takes as plesiomorphic a disjunct system in which a parivincular ligament representing F2 comprises the sole adult fibrous layer (Fig. 2.16A). A ligament system of this kind characterises at least some anomalodesmatan outgroups (e.g. Tellinidae and Donacidae among Euheterodonta, see Webb, 1986; Unionidae among Palaeoheterodonta, see Le Pennec & Jüngbluth, 1983; and numerous pteriomorphians, see Malchus, 2004). From this condition, all anomalodesmatan ligament grades may be derived:

1. The pholadomyoid ligament results from retention of F1 past the early juvenile stage, so that this layer remain visible at the anterior end of the adult ligamental apparatus (Fig. 2.16B).

2. In all other extant anomalodesmatan superfamilies calcification of F1 was observed and seems to be a consequence of retention of F1 in shells lacking a hinge plate. Because bivalve shells gradually splay apart as a result of marginal accretion (Stasek, 1963*a*), any structure attached to the internal walls of the umbonal cavity will rapidly increase in width. Under these circumstances, calcification of the sagittal portion of F1 divides its mechanical effort into two sectors of appropriate width to cross-sectional area ratio. Note that this functional explanation for the appearance of the lithodesma is virtually the same envisaged by Yonge & Morton (1980), but the process leading to a exceedingly wide internal ligament is heterochronic (retention of F1 towards later ontogenetic stages) rather than ventral migration of a fibrous ligament layer.

3. The ligament of *Thracia phaseolina* and other species of *Thracia* is equivalent to the pholadomyoid grade, but with a calcified F1 (Fig. 2.16D).

4. In numerous other *Thracia* the calcified F1 is absorbed following the onset of F2 so that it is absent from the adult hinge (Fig. 2.16C). This grade, it is hypothesised here, also characterises Poromyidae, even though direct evidence for a disjunct ligament with calcified F1 is lacking for this family. The hypothesis may be tested by studying the ontogeny of the ligament of poromyids and is supported by indirect evidence, namely the presence of ligaments comprising a calcified F1 in other septibranchs.

5. Laternulid and periplomatid ligament grades are achieved by the ventral migration of the parivincular ligament and its nymphs, forming an internal F2 supported by robust chondrophores. A graded morphological series linking typical nymphs to chondrophores is observed in extant thracioids, suggesting homology of these support structures. Variations in the expression of F1 are also observed here, several but not all taxa keeping the sagitally calcified layer into adulthood (Figs 2.16E, F).

6. Finally, the "lyonsiid" grade of Yonge & Morton, 1980, p. 288, present in Pandoroidea, Clavagelloidea, Verticordiidae, Cuspidariidae and several thraciid genera, is a paedomorphic system, characterised by the complete suppression of F2 (Fig. 2.16G). As such, it may be derived from virtually any of the preceding grades bearing a calcified F1.

The new model restricts the idea of ventral migration to the secondly formed fibrous layer (F2) and attempts to explain most of the disparity among anomalodesmatan ligament systems as a result of heterochronic alterations of a disjunct ligament.

Ventral displacement of F2, culminating in the robust chondrophores of periplomatids and laternulids is probably an adaptation for deeper burrowing. In other bivalve groups, compact internal ligaments, considerably reduced in antero-posterior length, have evolved primarily in deep-burrowing taxa (e.g. *Mya* and *Lutraria*), where they permit rocking of the valves about a dorso-ventral axis to ease the operation of large siphons (Trueman, 1964; Stanley, 1970) and the ejection of water during hydraulic burrowing (Checa & Cadée, 1997).

As for heterochronic changes, it was unfortunately not possible to assert which processes led to peramorphosis or paedomorphosis in each studied case. Each of these phenomena may be produced by changes in the rate of growth, onset time or offset time of the traits being studied, and confidently distinguishing between these possibilities

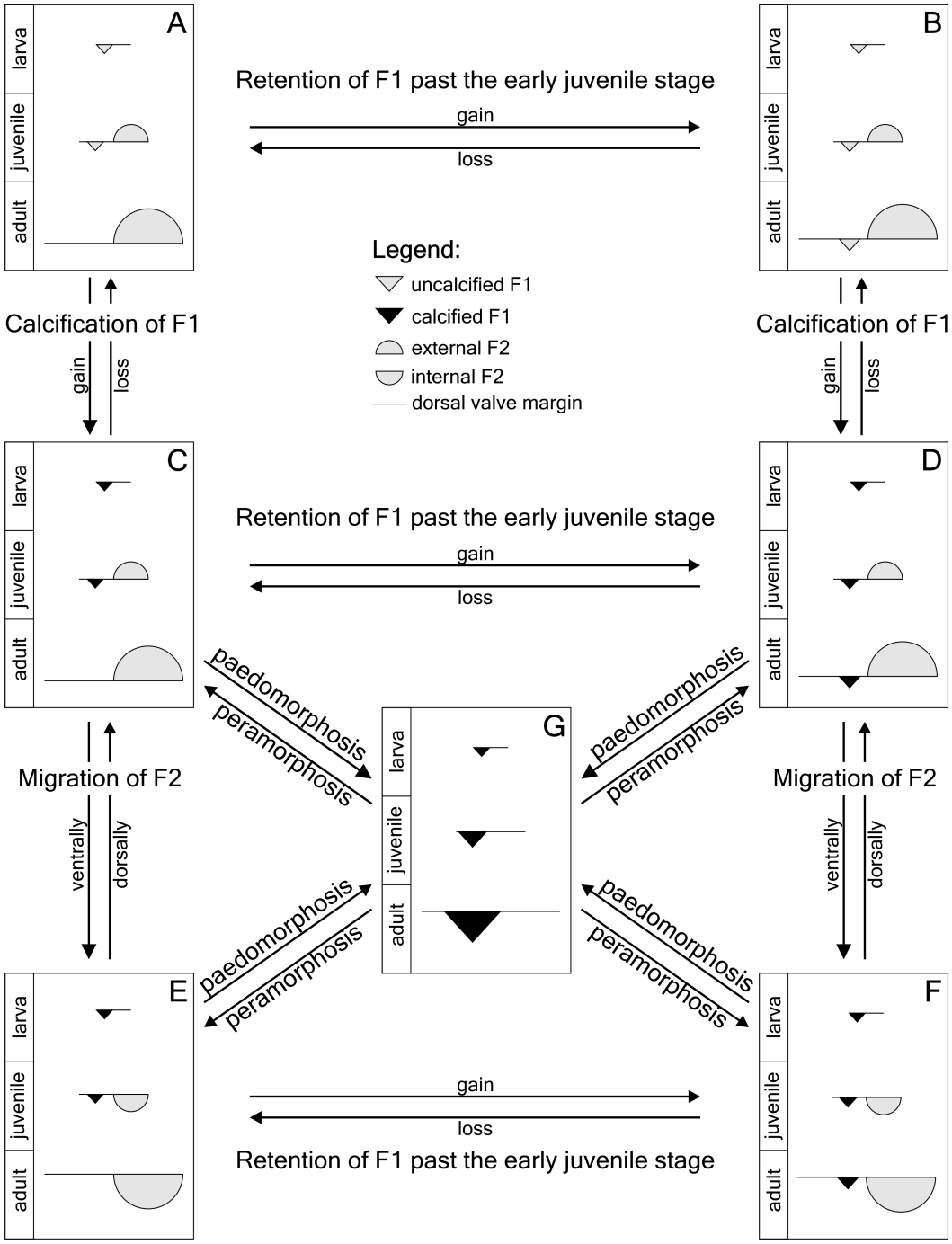


Figure 2.16: Hypothesized transitions between anomalodesmatan ligament grades (see text for details). Each grade is represented by diagrams of the hinge of the right valve (i.e. dorsum is towards the top and anterior end towards the left-hand side of the figure) of larval, early juvenile and adult stages. Grade **A** represents the ligament system presumed to characterise the common ancestor of crown-group Anomalodesmata. Grade **B** is displayed by Pholadomyoidea, and possibly by Palaeozoic Edmondioidea and Megadesmidae (see Waterhouse, 1969*a*). **C** characterises some species of *Thracia* and possibly poromyids. Grade **D** is displayed by numerous species of *Thracia*. **E** is found in some laternulids, whereas **F** is the commonest grade in both Laternulidae and Periplomatidae. **G** occurs in Pandoroidea, Clavagelloidea, Verticordiidae, Cuspidariidae and in some thraciids.

requires the age of specimens being compared to be known (Gould, 1977; McKinney & McNamara, 1991). In any case, the model draws attention to a hitherto unnoticed point — that heterochronic changes have probably played a major role in anomalodesmatan evolution.

Chapter 3

Form, function and evolution of the arenophilic glandular system

One of the only morphological features which seems exclusive of anomalodesmatans is a remarkable system of multicellular glands solely concerned with agglutination of foreign material. The glands, termed arenophilic by Prezant (1981*b*), discharge a bi-layered secretion of glycoprotein and acidic mucopolysaccharide which glues sediment particles onto the external surface of the periostracum. Despite their anatomical complexity, dedicated function and unparalleled occurrence, the use of arenophilic glands in systematic studies has been hindered by doubts regarding their homology and incomplete knowledge of taxonomic distribution.

The organs were first recorded in several members of the Verticordiidae (*sensu* Keen, 1969*a*) by Allen & Turner (1974), who described them as elongated, multicellular glands, discharging just inside the outer limit of the middle mantle folds. Allen & Turner (1974) tentatively ascribed them an adhesive function after observing sand grains and skeletal remains attached to the shell and mantle edge of species possessing these organs.

Prezant (1979*a*) observed similar glands in *Lyonsia hyalina* and conducted pioneering work on their anatomy, histochemistry and ultrastructure which confirmed a dedicated role in sediment adhesion. He subsequently surveyed laternulid, thraciid, pandorid, periplomatid and additional lyonsiid taxa, but found arenophilic glands absent in all but the last of these families (Prezant, 1981*b*). Prezant (1981*b*) claimed lyonsiid arenophilic glands were derived from the outer mantle folds and reported striking differences in the position of their opening in *Lyonsia* and *Entodesma*, asserting that whilst in the former genus glands discharge directly on top of the periostracum, being

hence quite similar to those of verticordiids, in the latter they open beneath the periostracum and must perforate the periostracal sheet to coat the external surface of the shell with adhesive. The close correspondence between *Lyonsia* and verticordiids led Prezant (1981*b*, p. 286) to argue for homology of the arenophilic system, maintaining "it is unlikely that such specialised glands arose separately in two such similar bivalve families". Paradoxically, however, in the following page of the same paper Prezant (1981*b*) suggested two independent origins of arenophilic glands in lyonsiids based on the distinct configuration recorded in *Entodesma*.

Meanwhile, Morton (1980, 1981*b*, 1982, 1984*a*) maintained that pholadomyids lack arenophilic glands and registered the occurrence of the organs for the first time in the families Periplomatidae, Parilimyidae and Clavagellidae. In a subsequent paper, Morton (1987*b*) re-evaluated the anatomy of the arenophilic system in *Entodesma*, arguing that glands in the genus occupy the same position as those of other anomalodesmatans, i.e. in between outer and middle mantle folds, and, likewise, discharge on top of the periostracum. Because arenophilic glands border both mantle folds, Morton (1987*b*) concluded that, in the absence of further evidence, hypotheses deriving the arenophilic system from either outer or middle folds seemed equally feasible.

In recent years, Harper *et al.* (2006) mapped arenophilic glands on the topology of their 18S rRNA Maximum Likelihood tree of anomalodesmatan relationships, constrained for monophyletic septibranchs. Distribution of the states suggested two independent origins followed by multiple losses of the organs in the group.

This chapter reviews the anatomy and histology of the arenophilic gland system and considerably expands the known taxonomic distribution of the organs in extant anomalodesmatans by describing the hitherto unknown arenophilic systems of laternulids and pholadomyids. Additionally, preserved arenophilic secretion is for the first time recorded in fossil anomalodesmatans, providing direct evidence that arenophilic systems had evolved by the early Jurassic. Derivation of the glands from the middle mantle fold and a single evolutionary origin for these organs are favoured based on novel evidence. Most of these data are published in Sartori *et al.* (2006) and Sartori & Harper (2009).

3.1 Material and methods

3.1.1 Extant material

3.1.1.1 Observations *in vivo*

Observations *in vivo* were undertaken on specimens of *Laternula elliptica* collected by SCUBA divers from Rothera Point, Adelaide Island, Antarctica (67°34' S; 68°08' W), and kept in the British Antarctic Survey Marine Aquarium for 9 months (Peck, personal communication 2005; see Ward & Peck, 1997, for details of the holding conditions). Animals were placed in a tank with sediment and seawater at 0 ± 1 °C and the morphology and behaviour of arenophilic papillae on their siphons observed under a dissecting microscope.

3.1.1.2 Observations of dried shells and preserved soft parts

All taxa surveyed for the presence of an arenophilic system are listed in table 3.3, with a reference to "Original observations". Collection data and other details of the analysed specimens can be found in Appendix A, which also provides a guide to institutional abbreviations cited in figure captions.

Material represented solely by hard parts had its external surface checked under a dissecting microscope for secretion from the glands. Some shells were also studied under a JEOL 820 scanning electron microscope after being ultrasonically cleaned for 1–5 minutes, air-dried for 48 hours and gold-coated.

Mantle and siphons of specimens with preserved soft parts were examined under a dissecting microscope in the search for arenophilic glands, whose topology, anatomy and histology were then studied. Specimens selected for histological investigation had their shells and other hard parts either carefully excised during dissections or decalcified by immersion in 0.25% acetic acid. They were subsequently dehydrated in a graded ethanol series, treated with xylene and embedded in paraffin wax. The resulting blocks were serially sectioned at 7 μm and the sections mounted on microscope slides and stained with haematoxylin and eosin.

Due to the paucity and historical importance of specimens of *Pholadomya candida* in museum collections, destructive techniques were not applied to individuals of this species. Instead, all material available in the collections of the Natural History Museum, London (BMNH) and Zoological Museum of the University of Copenhagen (ZMUC)

were carefully studied, including histological sections of the mantle margins prepared and previously reported upon by Morton (1980).

3.1.2 Fossil material

Fossil anomalodesmatans were examined in the collections of the Sedgwick Museum, Cambridge University, U.K. (CAMSM). Attention was focussed on well-preserved material, where at least part of the original aragonitic shell is present. Specimens were initially analysed with hand lenses (10x and 20x magnification) and those suspected to exhibit preserved arenophilic secretions on the external surface of their shells further studied under a dissecting microscope.

3.2 Arenophilic system in extant forms

Even though modern anomalodesmatans exhibit numerous variations in the organisation of their arenophilic apparatus, a general pattern can be clearly recognised. Hence, to avoid unnecessary repetition, detailed accounts will be only given herein of the previously unknown systems of laternulids and pholadomyids. These descriptions, complemented with data obtained from other taxa and the literature, will form the basis of a comparative analysis and discussion of the topology, histology and pallial origin of the glands in anomalodesmatans.

3.2.1 Laternulidae

All species of *Laternula* possess conjoined siphons formed by fusion of the three marginal mantle folds (type C of Yonge, 1982). Fusion includes the periostracal groove, which is thus positioned near the distal tips of the siphons, accounting for the thick periostracal sheet that surrounds their lateral walls (Fig. 3.1). This layer of periostracum is further enveloped by a coat of sediment particles and organic debris bound by numerous thin threads (Fig. 3.2A, B) arranged in longitudinal arenophilic lines along the length of the siphons (Fig. 3.2C). Threads may be either individually attached to the periostracum (Fig. 3.2A) or, more commonly, bear a conjoined base that forms a main strand of secretion. In *L. truncata* and *L. boschasina*, and to a lesser extent in *L. elliptica* and *L. marilina*, arenophilic threads extend over the space between main strands, often forming an almost continuous adhesive web over the periostracum that covers the siphonal walls (Fig. 3.2D).

Figure 3.1: Left view of *Laternula truncata*, showing the dense coating of sediment particles on the periostracum that envelops the fused siphons of the species, and the lack of debris on the general shell surface.

Each arenophilic line is secreted by a gland opening onto a papilla in the distal tips of the siphons. Glands and papillae are uniformly distributed along a ring that runs adjacent to the periostracal groove, surrounding not only the inhalant and exhalant apertures, but also the space in between these apertures (Fig. 3.3). Shape and dimensions of the glands are remarkably similar along the extent of this ring.

Arenophilic papillae are short and rounded in *L. elliptica*, whereas in *L. truncata* they are elongate and very similar in overall shape to the outermost inserted tactile tentacles of the siphons. Papillae may be distinguished from the tentacles for bearing a longitudinal slit that faces the periostracal groove and corresponds to the discharge point of the contained arenophilic gland. Width of the longitudinal slit presumably determines the thickness of the arenophilic threads because secretion from the gland must pass through this pore to reach the surface of the periostracum. Specimens of *L. boschasina* and *L. marilina* were too contracted to allow for a reliable description of papillae morphology. However, histological sections confirmed their position and abundance. Arenophilic glands (and their respective papillae) of *L. marilina*, *L. elliptica* and *L. truncata* are numerous and continuously distributed along the ring that accompanies the periostracal groove (Fig. 3.4A) whilst in *L. boschasina* glands are more spaced out and fewer (Fig. 3.4B) in number. In all investigated species arenophilic papillae are formed by the middle mantle folds, and the contained glands discharge their content directly onto the outer surface of the recently secreted periostracum.

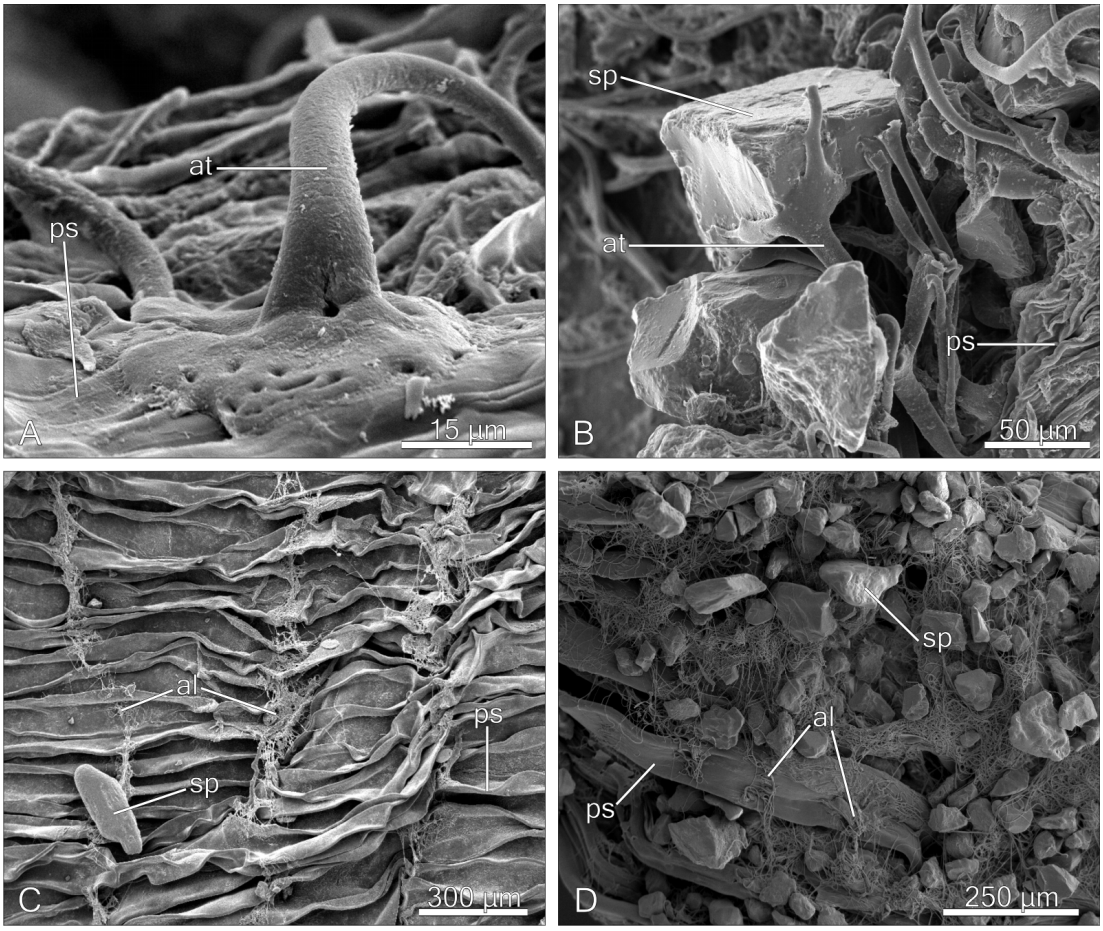


Figure 3.2: Scanning electron micrographs of the external surface of the periostracum covering the siphons of *Laternula*. **A**. *L. boschasina*. Detail of the proximal tip of an arenophilic thread linked to the periostracum. **B**. *L. elliptica*. Detail of the distal tip of some arenophilic threads bound to sediment particles. **C**. *L. marilina*. Adjacent lines of arenophilic secretion. **D**. *L. truncata*. Arenophilic threads extend in between the lines, forming an almost continuous adhesive web over the periostracum. Abbreviations: **al**, arenophilic lines; **at**, arenophilic threads; **ps**, periostracum surface; **sp**, sediment particles.

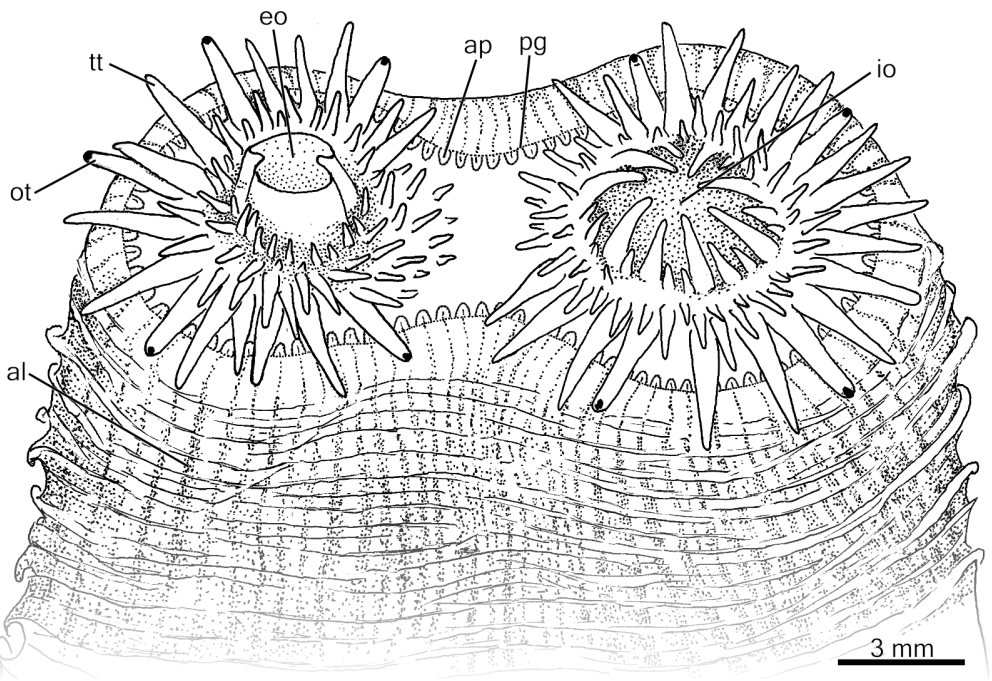


Figure 3.3: *Laternula elliptica*. Siphons viewed from the left side, showing the position of the arenophilic papillae and periostracal groove. Abbreviations: **al**, arenophilic line with adhered sediment particles; **ap**, arenophilic papilla; **eo**, exhalant opening; **io**, inhalant opening; **ot**, optic tentacle; **pg**, periostracal groove; **tt**, tactile tentacle.

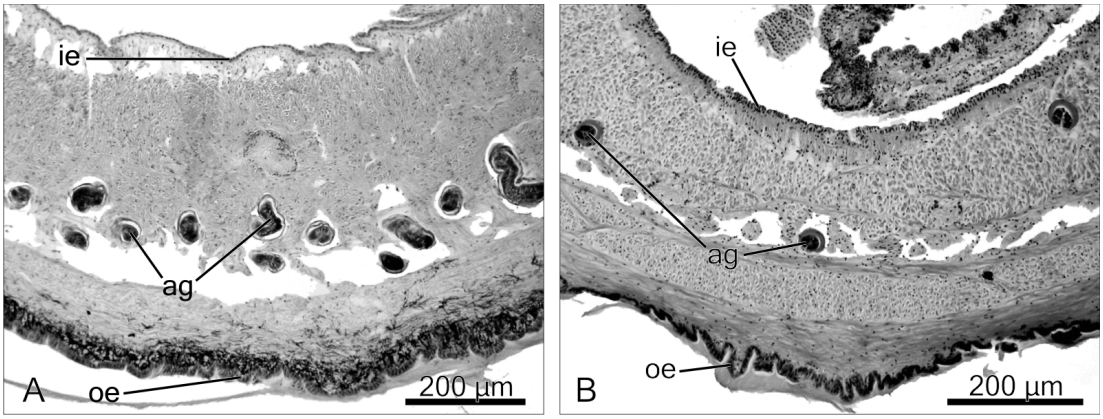


Figure 3.4: Light micrographs of transverse sections through the siphonal walls of *Laternula truncata* (**A**) and *L. boschasina* (**B**), showing the distribution and abundance of arenophilic mantle glands. Abbreviations: **ag**, arenophilic mantle glands; **ie**, inner epithelium; **oe**, outer epithelium.

Living specimens of *L. elliptica* are capable not only of protracting and retracting their arenophilic papillae, but also of gently swaying their tips in all directions. Accordingly, histological sections through the papillae of all investigated laternulids revealed that they are largely composed of muscular tissue, with fibres arranged in both transverse and longitudinal bundles, but not directly linked to the contained glands (Fig. 3.5A). Swaying of the discharge point of the glands during secretion results in the tips of the arenophilic threads being laid away from the main longitudinal strand of secretion, accounting for the web-like distribution of the threads.

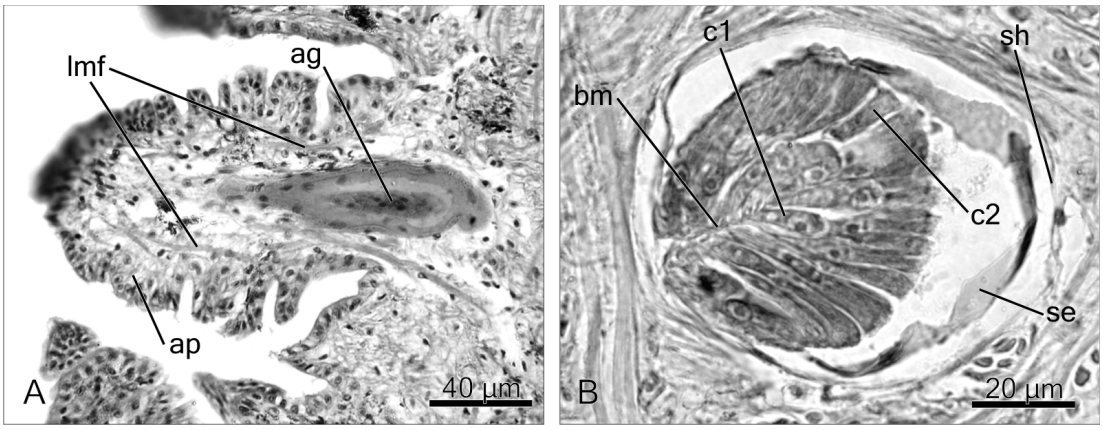


Figure 3.5: **A**. *Laternula boschasina*. Light micrograph of a frontal section through an arenophilic papilla, showing its musculature. **B**. *L. elliptica*. Light micrograph of a transverse section through an arenophilic gland, showing its structure. Prepared in collaboration with Flávio D. Passos and Osmar Domaneschi (Universidade de São Paulo) Abbreviations: **ag**, arenophilic mantle gland; **ap**, arenophilic papilla; **bm**, basal membrane; **c1** and **c2**, cell types 1 and 2 of the secretory core; **lmf**, longitudinal muscle fibres; **se**, secretion; **sh**, sheath of squamous epithelium.

In all laternulids, the glands comprised a club-shaped core of secretory cells surrounded by a thin sheath of squamous epithelium (Fig. 3.5B). The core is composed of a pseudostratified epithelium formed by two cell types. Type 1 cells are basophilic and ovoid, with a distally positioned nucleus, and occupy a central posititon in the gland, not contacting the periphery of the core. Type 2 cells are elongate, roughly pyramidal, with a medially positioned nucleus, and stain even more basophilically than type 1 cells (Fig. 3.5B).

The core of the glands is considerably larger in *L. elliptica* than in the remaining representatives of the genus (Table 3.1). Maximum lengths recorded for arenophilic glands in *L. marilina*, *L. truncata* and *L. boschasina* were 570, 1040 and 1310 μm, respectively. Length of the glands was not measured in *L. elliptica* due to the lack of

Table 3.1: Diameter of the core of the arenophilic glands of *Laternula marilina*, *L. truncata*, *L. boschasina* and *L. elliptica*.

	Diameter (μm) mean ± SD	No. of glands measured
Laternula marilina	26.2 ± 5.9	4
Laternula truncata	27.2 ± 3.0	15
Laternula boschasina	32.2 ± 3.6	8
Laternula elliptica	67.8 ± 7.1	9

longitudinal histological sections through the siphonal tips. Preservation of the studied taxa in different fixatives might have accounted for part of the variation observed in gland dimensions among species.

The remaining extent of the mantle of adult laternulids, i.e. ventral and anterior margins, is devoid of arenophilic glands. Nonetheless, two arenophilic glands were found along the ventral mantle margins of a juvenile *L. elliptica* measuring 17 mm in shell length (adults may grow to 120 mm; see Urban & Mercuri, 1998). Both glands measured ~230 μm in length and were located in the edge of the right mantle lobe, one roughly in the middle of the pedal opening, the other immediately posterior to it. They are located proximal to the innermost cells of the periostracal groove, between the outer and middle marginal mantle folds and, thus, discharge their secretion directly onto the outer surface of the periostracum (Fig. 3.6A). These glands seem to be either vestigial or to perform a modified function in juveniles because the shell surfaces of *L. elliptica* and other laternulids lack radially disposed lines of sand grains. Even though some loose patches of adhered debris are seen in some specimens, attachment of these particles to the shell surface is never mediated by the threads that characterize secretion from arenophilic mantle glands (Fig. 3.6B).

3.2.2 Pholadomyidae

Runnegar (1972) and Morton (1980) described the surface ornamentation of the shell of *P. candida* as comprising broad radial ribs with tubercles, deep commarginal undulations, and rows of tiny granules, but failed to note a series of fine arenophilic lines, distributed radially throughout the entire surface of the valves, which was found present in all specimens analysed herein (Figs 3.7A, B). These lines are spaced approximately a half to three millimetres from each other along the posterior and remaining margins of the shell, respectively. They range in colour from light yellow to dark brown, rarely

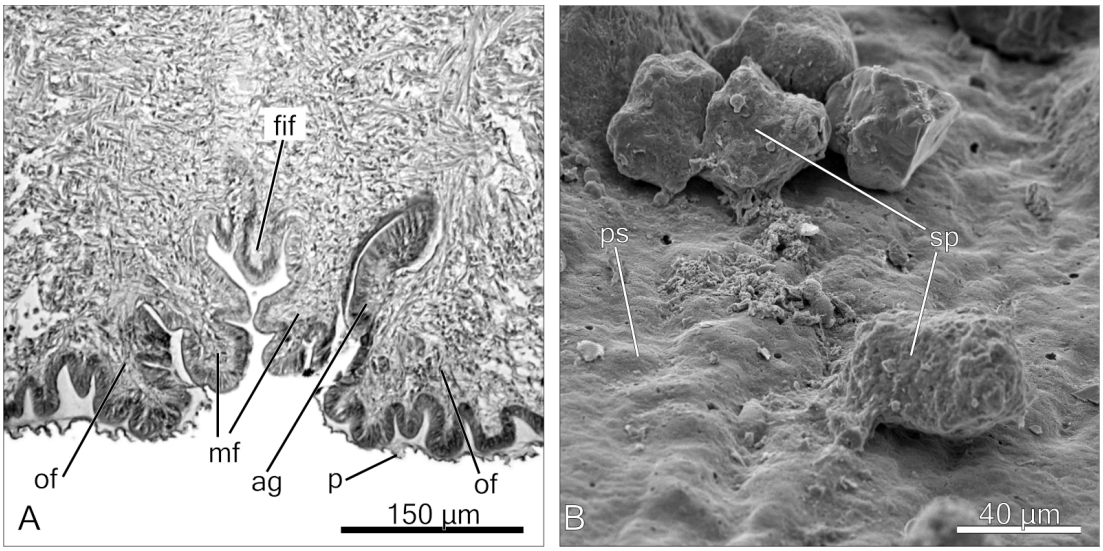


Figure 3.6: **A**. *Laternula elliptica*. Light micrograph of a transverse section through the fused mantle margins of a juvenile specimen (shell length = 1.7 cm), showing an arenophilic mantle gland in the right mantle lobe. Prepared in collaboration with Flávio D. Passos and Osmar Domaneschi (Universidade de São Paulo). **B**. *L. truncata*. Scanning electron micrograph of the external surface of the shell, showing sediment particles bound to the periostracum. Abbreviations: **ag**, arenophilic mantle gland; **fif**, fused inner mantle folds; **mf**, middle mantle folds; **of**, outer mantle fold; **p**, periostracum; **ps**, surface of the periostracum; **sp**, sediment particles.

exceed 0.3 mm in width, and are less evident in the oldest, worn portions of the shell (typically from the umbones to approximately the middle of the valves' height). Each line comprises a main strand which follows a meandering trail on the shell surface, and from which numerous threads project in every direction, forming characteristic tufts (Fig. 3.7C). Such an arrangement closely resembles the lines of secretion displayed by taxa with well-developed arenophilic systems, such as species of *Lyonsia* (Fig. 3.7F). However, none of the specimens of *P. candida* available for study displayed debris attached to the shell, a common feature in species bearing arenophilic glands (Fig. 3.7E).

Nonetheless, it is important to note that mollusc shells in museum collections, particularly in the past, have often been carefully cleaned in the belief that all sediment encrustations are inorganic and irrelevant to the animal (Taylor *et al.*, 1999). All specimens of *P. candida* analysed herein and most of those figured in the literature were collected in the early 19th Century and held in high regard by their holders (Dance, 1969), so it seems rather likely that any adhering sediment would have been removed. Significantly, a dense layer of sediment particles is visible covering much of the shell of a freshly collected individual of *P. candida* illustrated by Diaz *et al.*, 2009, fig. 1).

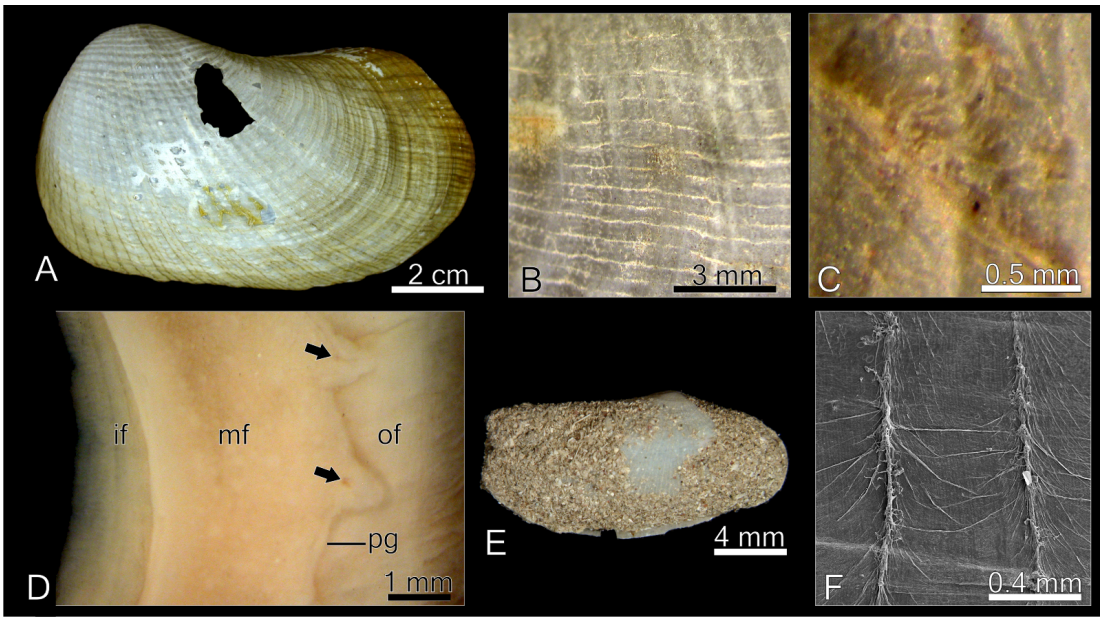


Figure 3.7: Aspects of the arenophilic system of the extant anomalodesmatans *Pholadomya candida* (**A-D**), *Lyonsia norwegica* (**E**) and *L. floridana* (**F**). **A**. External view of the left valve, showing the distribution of radial lines of arenophilic secretion (BMNH 1969266). **B**. Detail of the lines of arenophilic secretion on the posterior end of the left valve; posterior margin toward the right hand side (ZMUC; Tortola). **C**. Close up of one arenophilic line, showing secondary threads radiating from the main strand of secretion (ZMUC; specimen with soft parts preserved). **D**. Ventral view of the right margin of the pedal aperture, showing the middle mantle fold papillae and associated discharging openings of arenophilic glands (arrows). **E**. Right view of the shell, showing a dense cover of sediment particles bound to radial lines of arenophilic secretion (BMNH 1911.10.26.50090-50109). **F**. Scanning electron micrograph of the external surface of the shell, showing two arenophilic lines with numerous secondary threads radiating from the main strand of secretion; shell margin toward the bottom (FMNH 288890). Abbreviations: **if**, inner mantle fold; **mf**, middle mantle fold; **of**, outer mantle fold; **pg**, periostracal groove.

In any case, if the radial lines of *P. candida* are indeed part of an arenophilic system, their distribution on the shell surface must match that of glands in the animal's soft parts. Examination of the mantle margins revealed large, muscular papillae in the middle folds whose distribution and spacing was compatible with the radial lines (Fig. 3.7D, 3.8A; "SP" in Morton, 1980, figs 8, 9, 10, 14). Threads of secretion coming out of an opening on the inner surface of several of these papillae confirmed the presence of arenophilic glands. The latter are formed as invaginations of the mantle epithelium and comprise two distinct regions, the secretory core and the sheath (Fig. 3.8B). Cells comprising the secretory core are much taller than their neighbours and seem to form a central ring, approximately mid-way in between the discharge opening and the proximal end of the gland. The sheath comprises squamous cells and extends from the core to

the proximal end, possibly functioning in retaining the glandular secretions and/or shaping them into threads. Unfortunately, further histological and cytological details could not be obtained due to the poor preservation of the tissue, which were fixed suboptimally although, considering that the specimen was collected and preserved in 1835 and sectioned nearly 30 years ago (Morton, 1980), the appearance of the material is surprisingly good.

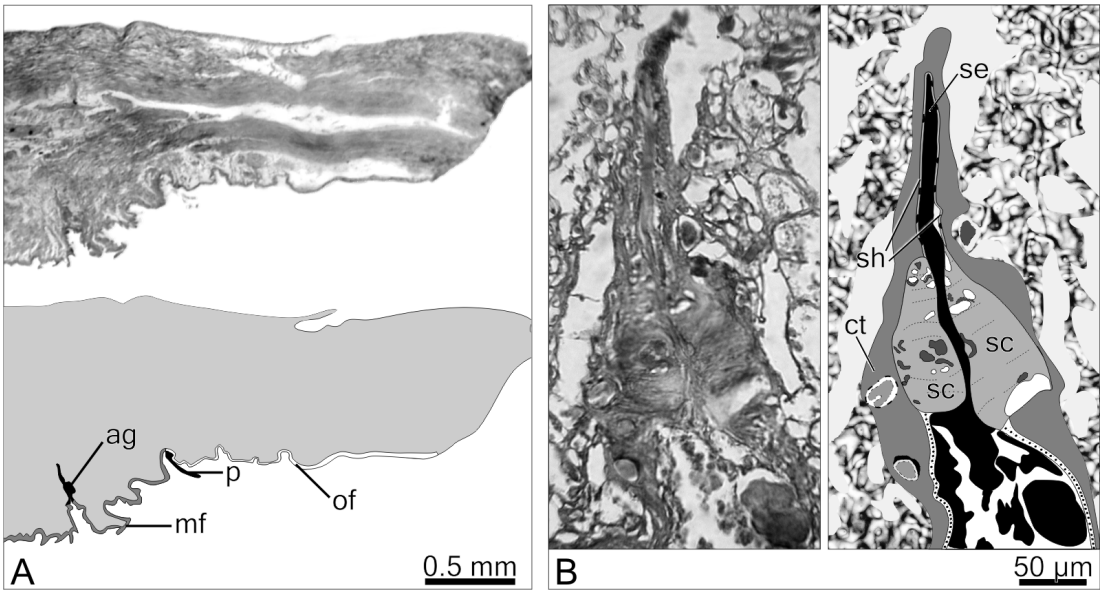


Figure 3.8: *Pholadomya candida*. Photographs and interpretative drawings of a transverse section through the ventral mantle margins, showing the topology (**A**) and histology (**B**) of the arenophilic glands (ZMUC; specimen with soft parts preserved; slide 24 of the series "T.S. ventral mantle"). Abbreviations: **ag**, arenophilic gland; **ct**, connective tissue; **mf**, middle mantle fold; **of**, outer mantle fold; **p**, periostracum coming out of the periostracal groove; **sc**, secretory core; **se**, secretion; **sh**, sheath.

3.2.3 Comparative anatomy

3.2.3.1 Corporeal distribution

In the vast majority of extant anomalodesmatans arenophilic glands are found throughout the entire extent of the mantle edge although they are commonly more numerous along the pedal aperture and posterior, siphonal margin. This is the case, for instance, in *P. candida* described above and *Lyonsia californica*, estimated to bear more than 40 glands surrounding its siphons (Prezant, 1981*b*). Only clavagelloids (Morton, 1984*a*,*b*, 2002*b*) and laternulids (this study) are known to display the organs restricted to the

siphonal tips in adult specimens, but both taxa may display more or less evenly distributed glands in earlier ontogenetic stages. Harper & Morton (2004, fig. 3a) described and illustrated lines of arenophilic secretion on a juvenile shell of *Penicillus penis* radiating from the beaks to the boundary between juvenile shell and saddle, which provide compelling evidence that the species bears a functional, evenly distributed arenophilic system before becoming tubiculous. Similarly, the discovery of two glands in the vicinity of the pedal opening of juvenile *L. elliptica* but none in adults, reported above, suggests that laternulids too may bear glands throughout their mantle margins in early life, which are progressively lost as the animal grows. Ontogenetic regression in the number of arenophilic glands has also been recorded in species of *Entodesma* but in this lyonsiid genus they are not selectively reabsorbed from certain areas of the mantle while thriving along others (Prezant, 1981*b*, 1985*a*).

Loss of arenophilic glands along the general mantle margins appears to be one of many marked morphological changes that precede formation of the adventitious tube during the life cycle of clavagelloids. Harper & Morton (2004) studied the adventitious tube of *Brechites vaginiferus* and showed that the structure is not extra-periostracal as had been hypothesised by Morton (1985*a*), but forms within a periostracal sheet via "normal" shell-secreting mechanisms. Thus, in order to secrete a continuous calcareous ring around their bodies, clavagelloids must fuse their lateral periostracum and shell secreting epithelia, i.e. their left and right outer mantle folds. Such a degree of mantle fusion (type C of Yonge, 1957) is, of course, incompatible with a functional arenophilic system because, enveloped by the wall of the forming tube, glands would now be unable to pour their adhesive secretion on the external surface of the periostracum. Confinement of the arenophilic glandular system to the siphonal tips of clavagelloids is therefore a requirement for construction of the adventitious tube.

Presence of functional glands in early juvenile clavagelloids implies, likewise, that mantle fusion at that stage must either be lacking or involves solely inner and middle folds (types A and B of Yonge, 1957). Unfortunately, however, suitable material to test this hypothesis is presently unavailable. Illustrations by Smith (1910, fig. 1) and Morton (2002*b*, fig. 2a) of the only juvenile clavagelloid preserved in museum collections clearly show that great part of the saddle had already been secreted at the time of preservation so that loss of the arenophilic system and progression of the degree of mantle fusion must have already taken place. Significantly, Morton (1984*b*) analysed the gross anatomy of this specimen and remarked that, except for the pedal and siphonal openings, its body is entirely enclosed in a periostracal sheet. Acquisition of clavagelloids at earlier

ontogenetic stages is thus required before the assertion that loss of the arenophilic system in the taxon occurs as a consequence of increasing degrees of mantle fusion can be tested appropriately.

Representatives of *Laternula* retain mantle fusion of type B throughout life so that loss of the arenophilic system along their ventral mantle margin cannot be seen purely as a constructional requisite but may instead have some ecological significance. Numerous hypotheses for the function of the sediment cover that results from activity of the glands have been suggested but none experimentally demonstrated. Nevertheless, all logical interpretations of the morphology of the coat favour stabilisation in shifting sediments and protection against predators as its most likely roles. In burrowing organisms, the likelihood of being dislodged by sediment scour or attacked by predators steeply decreases with increasing depths of burial and it is therefore significant that morphological adaptations to resist these hazards, in particular pronounced external ornamentation, prevail among shallow-burrowing bivalves (see Stanley, 1970; Vermeij, 1987). Except for the Antarctic *L. elliptica*, which is often found exposed at the sediment surface, presumably due to ice scour and other forms of disturbance (Peck *et al.*, 1999; Harper & Peck, 2003), species of *Laternula* are deep-burrowers that typically inhabit stable environments, where they are little likely to be completely exposed by erosion of the sediment (Savazzi, 1990; Peck *et al.*, 2004; Morley *et al.*, 2007; Prezant *et al.*, 2008). However, similarly to most other infaunal bivalves, *Laternula* must maintain the tips of the siphons exposed at the sediment surface during filter feeding, in a more vulnerable position than the remaining body parts. This mode of life arguably explains both retention of arenophilic glands on the siphons for camouflage and protection against predators, and concomitant loss of the organs along the remaining extent of the mantle margins because hindrance to burrowing would probably outweigh any benefit of a dense sediment cover on the surface of a deep-burrowed shell.

Whatever the functional significance of the arenophilic system of laternulids may be, it is clear that its restricted corporeal distribution in adult specimens has contributed to postpone their discovery until now, especially because comprehensive histological surveys of laternulids taxa by Morton (1973*a*) and Prezant (1981*b*) were carried out before publication of the first description of arenophilic glands confined to the siphonal tips of an anomalodesmatan (Morton, 1984*a*).

3.2.3.2 Histology and cytology

The histological and cytological aspects of arenophilic glands in distinct anomalodesmatan lineages appear generally similar, although Prezant's (1979*a*; 1981*b*) pioneering papers on lyonsiids remain the only to include ultrastructural details of the component cells and a preliminary chemical characterisation of their secretion.

In most anomalodesmatans the glands comprise an elongated core of tall secretory cells, surrounded by a thin sheath of squamous epithelium (Figs 3.5B, 3.6A, 3.9) which, at least in lyonsiids (Prezant, 1979*a*, 1981*b*), is also secretory. Seemingly distinct configurations have been illustrated for some but not all verticordiids studied by Allen & Turner (1974, figs 50, 73 and 80d) and recorded in *P. candida* during the present investigation. However, in both cases it remains uncertain whether differences are real or methodological artefacts.

Material studied by Allen & Turner (1974) was collected in deep waters by several scientific expeditions and its history of preservation and curation is unknown. Besides, the taxonomic focus of Allen & Turner's (1974) monograph and the large number of species being treated required the authors to undertake only a cursory study of most body parts. As Morton (1981*a*, p.48) points out in his study of arenophilic glands in the periplomatid *Offadesma angasi*: "the description by Allen & Turner (1974) of similar glands in the mantle of members of the Verticordiidae is insufficiently detailed to facilitate comparison". The same criticism applies to a recent revision of the verticordiid genus *Spinosipella* by Simone & Cunha (2008).

The glands of *P. candida*, with the secretory core organised around a ring in between the discharge opening and proximal sheath (Fig. 3.8B), could well represent an authentic morphological variation of the anomalodesmatan arenophilic system. After all, the fused portion of the mantle margins of *P. candida* is distinctly wider than that of other extant anomalodesmatan taxa (Morton, 1980, fig. 8), except parilimyids (Morton, 1982, fig. 19), and so the compact arrangement of the most taxonomically widespread gland type could have resulted from compaction of the mantle margins due to increasing degrees of mantle fusion. Nevertheless, I cannot dismiss the possibility of differences being at least in part artefactual, due to the poor preservation of the histological sections of *P. candida* that are available for study. Confirmation of the histological organisation and further studies of the glands of the species must await examination of freshly collected and well-preserved material.

3.2.3.3 Topology and pallial origin

In all studied anomalodesmatans but *P. candida*, the secretory core of the arenophilic glands is adjacent to the periostracal groove (e.g. *L. elliptica*, Figure 3.6A; *Lyonsia norwegica*, Figure 3.9), which marks the limit between outer and middle mantle folds (Yonge, 1957). Epithelial continuity with both mantle sectors allowed authors to envisage the origin of the glands from either an invagination of the middle folds (e.g. Allen & Turner, 1974; Morton, 1984*a*, 2002*b*) or from cells of the outer folds which primitively secreted periostracum (e.g. Prezant, 1981*b*, 1985*b*, 1998*b*). Arguments in favour of the latter possibility include (1) Prezant's (1981*b*) observation of arenophilic glands contained within the limits of the outer folds of representatives of the lyonsiid genus *Entodesma* and (2) derivation of glands from cells which were already performing a secretory function would seem more likely than from elsewhere (Prezant, personal communication 2008).

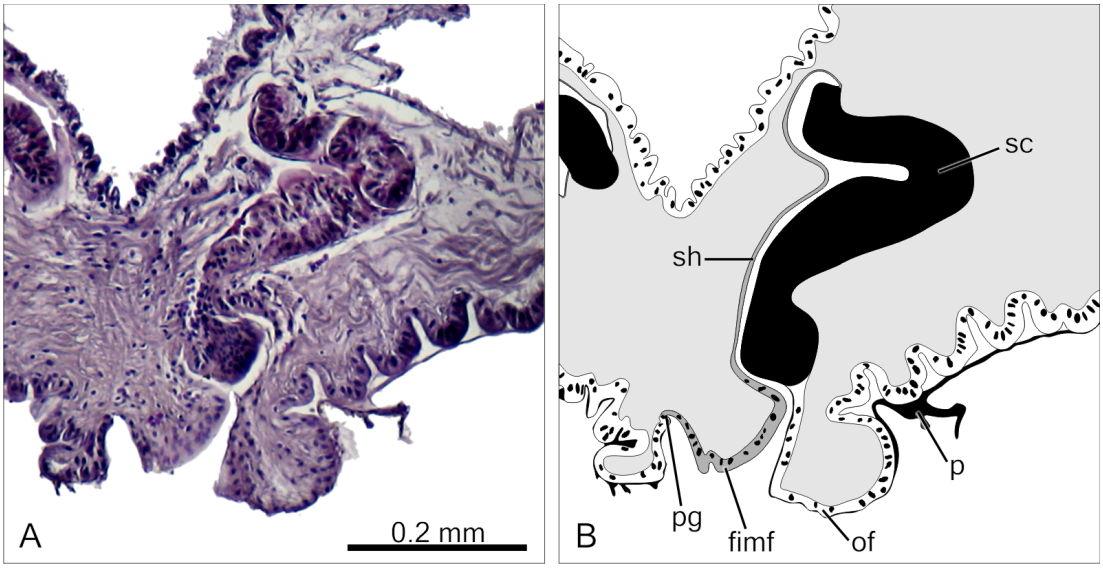


Figure 3.9: *Lyonsia norwegica*. Photograph (**A**) and interpretative drawing (**B**) of a transverse section through the ventral mantle margins, showing the topology of an arenophilic gland (BMNH 20070070, series 3). Abbreviations: **fimf**, fused inner and middle mantle folds; **of**, outer mantle fold; **p**, periostracum; **pg**, periostracal groove; **sc**, secretory core of the gland; **sh**, sheath of the gland.

However, claims of a different arrangement in *Entodesma*, with glands opening under the periostracal sheet and periodically secreting an unknown protease to perforate that sheet (Prezant, 1981*b*), are not only overly complex but have been dismissed as an artefact by a subsequent investigator (Morton, 1987*b*). A false image of periostracum

penetration in isolated histological sections arises when the plane of section includes the discharge point of the gland amid periostracum secreting epithelia. Consequently, the higher the proportion of a gland's perimeter which is surrounded by outer mantle tissue, the greater its likelihood of producing this artefact when sectioned. The fraction of a gland's opening bordered by outer mantle tissue is determined in part by its degree of contraction upon preservation — withdrawal of the mantle edge tends to bring all marginal folds closer — and, more importantly, by the particular morphology of arenophilic papillae in each taxon. Papillae vary considerably in size and shape, ranging from digitiform appendages that project well above the periostracal groove toward the middle mantle fold (e.g. in *L. elliptica*, Figure 3.3), to inconspicuous lateral extensions of middle fold epithelium, opening within an embayment of outer mantle fold tissue. Papillae structured in the latter fashion are more likely than not to render false images of periostracum penetration in conventional histological sections, as illustrated for *Lyonsia norwegica* in Figure 3.10. Because each glandular opening is positioned within an invagination of outer mantle fold epithelium, at the distal end of an offshoot of the main crest of middle fold tissue (Fig. 3.10A, B), most histological sections will fail to reveal the continuous connection between arenophilic gland and middle fold crest, giving the *impression* of a pore in the periostracal sheet (Fig. 3.10C). In these cases, anatomy of the glands is normally easier to interpret in whole preparations, studied under a stereo or scanning electron microscope, even though careful analysis of complete histological series will often lead to a few sections in which the topology of the glands is clear (Fig. 3.10D).

Regarding the second argument, while derivation of arenophilic glands from a secretory epithelium may indeed be favoured, it is clear that the entire surface of the mantle of bivalves is capable of secretory activity, despite the pervasive influence of Yonge's (1948*a*; 1982) broad functional division of the mantle margins into outer secretory, middle sensory and inner muscular folds. In species of *Thracia*, for example, siphons formed solely by the inner mantle folds produce mucus-lined tubes (Yonge, 1937; Sartori & Domaneschi, 2005, fig. 6), whereas Taylor *et al.* (1999) suggested the large and glandular middle and inner folds of *Granicorium* as sources of mucus for sediment agglutination.

Thus, there are obvious problems in the arguments put forward in favour of an origin within the outer folds, and topology of the organs is ambiguous. Morton (1987*b*) discussed this issue and concluded that, in the absence of further evidence, hypotheses deriving the glands from the outer or middle mantle folds seemed equally feasible.

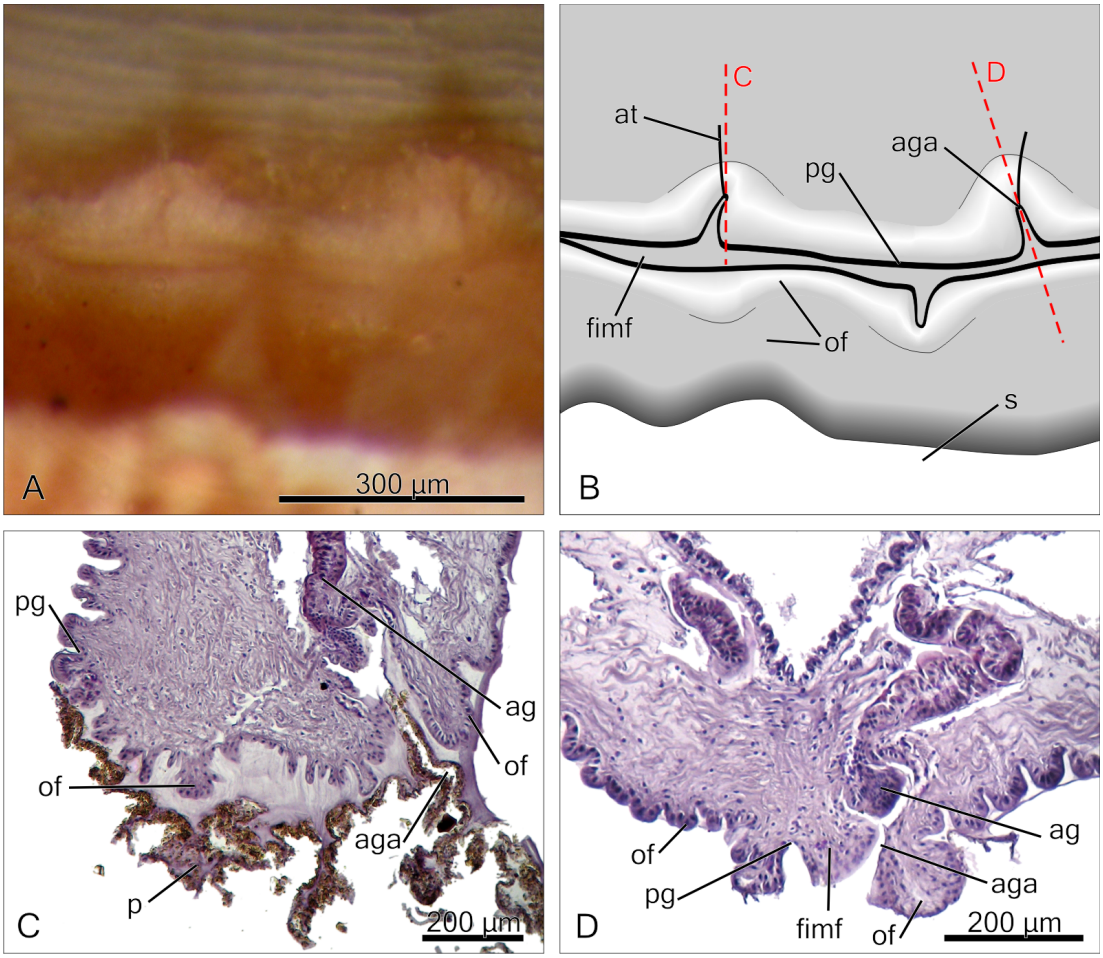


Figure 3.10: *Lyonsia norwegica*, BMNH 20070070. **A-B**. Photograph and interpretative drawing of the morphology of arenophilic papillae along the ventral mantle margin, respectively. **C-D**. Histological sections through the mantle margins, analogous to those indicated by the respective dashed lines in **B**. Abbreviations: **ag**, arenophilic gland; **aga**, aperture of arenophilic gland; **at**, thread of arenophilic secretion; **fimf**, fused inner and middle mantle folds; **of**, outer mantle folds; **p**, periostracum; **pg**, periostracal groove; **s**, shell margin.

Topology of the glands of *P. candida* casts new light on this debate. As showed herein, the glands of the species are internal to and well separated from the periostracal groove (Fig. 3.8A), being hence unambiguously contained within the middle folds. If the glands of *P. candida* are homologous to those of all other anomalodesmatans, as their similar organisation implies, then their occurrence in the middle folds of a member of the oldest and presumably most plesiomorphic extant anomalodesmatan family would strongly argue for an origin within this sector of the mantle margins. Migration of the glands closer to the outer folds in other anomalodesmatans was probably another consequence of compaction of the mantle margins due to increasing degrees of pallial fusion.

3.2.4 Recognition of arenophilic secretion

One of the most remarkable features of the anomalodesmatan arenophilic system are the fine lines of secretion laid on top of the periostracum, which match the position of each gland along the mantle margins. Surprisingly, however, following the very first description of arenophilic systems by Allen & Turner (1974), who produced several drawings and scanning electron micrographs of the lines, this character has been little explored. In fact, most subsequent detailed illustrations of the lines were included in papers that did not have the glands as their primary focus (e.g. Prezant, 1981*c*, figs 1,2; Harper, 1997, fig. 4d; Harper & Morton, 2004, fig. 3d). In *P. candida*, for instance, a species that has attracted considerable interest, arenophilic lines are rather conspicuous and actually visible in most of the many published illustrations of its shell (e.g. Sowerby, 1823, plate; Dance, 1969, pl. 23, b; Cox *et al.*, 1969, fig. 42-1b,c; Cox & Newell, 1969, fig. F9-1a,c; Waterhouse, 1969*a*, fig. 1a; Runnegar, 1979, fig. 2; Morton, 1980, figs 2a,b; 57 and pl. 1a,b,c). And yet, they have been invariably neglected in the numerous written descriptions of the species. Gibson-Smith & Gibson-Smith (1981, p. 356) were probably the first authors to note the arenophilic lines of *P. candida*, but they mistakenly interpreted them as part of the periostracum, describing the latter as "in the form of a filamentous mat with the filaments gathered along the crests of the radial ribs, and along the axes of the attendant interspaces, into a fine thread".

Virtually all records of arenophilic systems have relied on the discovery of the glands themselves in the animal's mantle margins. This has hindered the systematic use of these organs and limited our knowledge of their taxonomic distribution not only because glands can only be found in material containing soft parts, but also because they may be restricted in their corporeal distribution, inconspicuous under a stereomicroscope or

difficult to identify in histological sections. Recognition of arenophilic systems based on the presence of secretion on the surface of the periostracum offers a quicker, easier and inexpensive method, which has the additional advantage of being applicable to taxa represented by shell material only, both extant and fossil. Obviously, however, the method is only reliable if lines of arenophilic secretion can be confidently distinguished from other radially disposed elements of shell ornamentation, namely ribs running from the umbones to the margin, and rows of minute granules of calcified periostracum.

Granules will not be mistakenly interpreted as arenophilic lines unless they occur so close to each other within each row as to bear a conjoined base. To the best of my knowledge, such an arrangement has never been found in any anomalodesmatan.

Radial ribs are typically much wider than arenophilic lines, broaden gradually from the umbones to the shell margin and, because they are components of the shell wall, their profile will never be perfectly circular or detached from the shell surface. Additionally, being discharged from the base of muscular, motile papillae, arenophilic lines usually follow a sinuous trail on the shell surface whereas ribs are typically straight. Although injury of the mantle margins might lead to similar distortions in ribs, the two types of meandering are distinguishable because disturbance of the mantle affects not only the ribs but also the commarginal sculpture of the shell. In extant taxa, the colour and organic composition of the secretion, which readily dissolves when treated with a sodium hypochlorite solution (commercial bleach), as well as the flexible secondary threads that commonly project away from the surface of the periostracum, provide additional means of distinguishing arenophilic lines from radial sculpture formed by calcified periostracum or the shell wall proper.

Several of the additional records of extant arenophilic systems made during the present investigation were based on the recognition of the lines of secretion on the shell surface, following the criteria set out above (e.g. in *Thracidora arenosa*; Table 3.3). The same criteria allowed me to discovery, for the first time, instances of fossilised arenophilic secretion, as discussed in the section below.

3.3 Arenophilic system in fossil taxa

3.3.1 Records of fossilised arenophilic lines

Fossilised arenophilic secretion was identified in specimens of *Pleuromya* and *Pholadomya* from five different geological formations spanning in age from the early Jurassic to the Eocene (Table 3.2). Other fossil anomalodesmatans presenting suspect radial

Table 3.2: Specimens of *Pholadomya* and *Pleuromya* in the collections of the Sedgwick Museum, Cambridge, UK (CAMSM) showing evidence of preserved secretion from arenophilic glands.

Species	Formation	Locality	Accession numbers
Ph. margaritacea (J. Sowerby, 1821)	Barton Bed (Eocene - Bartonian)	Barton, Hampshire, England	C.56742, C.56752
	London Clay (Eocene - Ypresian)	Isle of Wight, Hampshire, England	C.16912
		Portsmouth, Hampshire, England	C.16923, C.16930, C.16931
Pholadomya sp.	Gault (Early Cretaceous - Aptian/ Albian)	Black Ven, Dorset, England	B.31775, B.31776, B.31777, B.31778, B.31780
Ph. cornueliana (d'Orbigny, 1844)	Early Cretaceous (Aptian)	La Presta, Val de Travers, Switzerland	F.5948
Ph. decorata Zieten, 1833	Early Jurassic (Middle Lias)	Bracebridge, Lincolnshire, England	J.41002
Pholadomya sp.	Early Jurassic (Middle Lias)	Bracebridge, Lincolnshire, England	J.41028
Pleuromya sp.	Swindon Clay (Late Jurassic - Kimmeridgian)	Swindon, Wiltshire, England	J.15780

features were not included here because either the number or morphology of their radiating features did not allow the hypothesis of artefacts of preservation to be confidently rejected.

In all specimens of fossil *Pholadomya*, lines of secretion were particularly evident at the posterior end of the valves, where radial ribs were lacking (Fig. 3.11A-C). Particularly well-preserved individuals from the early Cretaceous (Aptian-Albian) Gault Formation of the UK[1] showed lines occurring not only with the same arrangement and morphology in both the ribbed and smooth areas of the shell (Fig. 3.11D), but also in conjunction with minute granules (Fig. 3.11E), thus providing direct evidence that the

[1]labelled as *Pholadomya fabrina* d'Orbigny in CAMSM but the latter name is unavailable for being an incorrect subsequent spelling of *P. favrina* Agassiz, 1842, generally regarded as a junior synonym of *P. gigantea* (J. de C. Sowerby, 1836) (e.g., by Lazo, 2007). However, specimens in CAMSM and d'Orbigny's illustration of *P.* "fabrina" appear rather distinct from *P. gigantea* for bearing tubercles at intersections of radial ribs with commarginal undulations, and may belong to a different species. Until uncertainties are elucidated by a revision of d'Orbigny's material, I prefer to refer to this lot as *Pholadomya* sp.

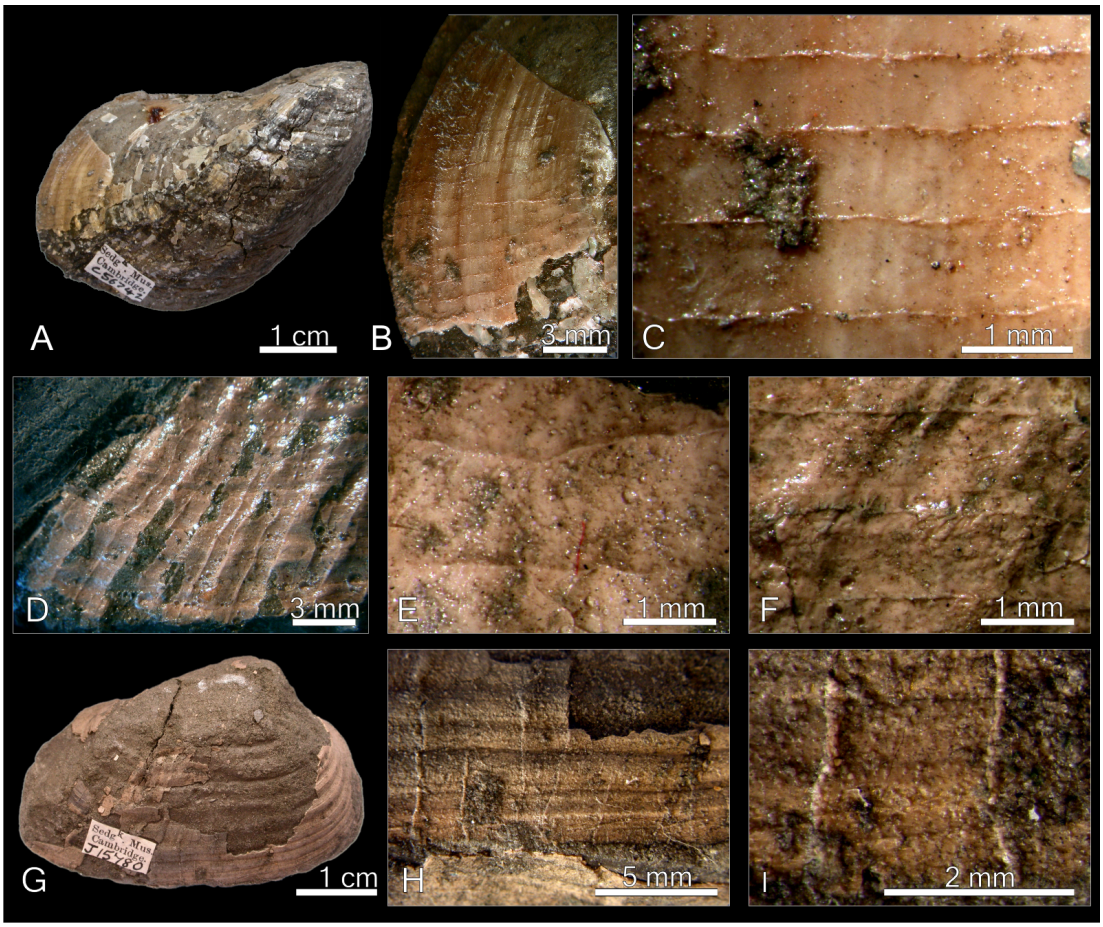


Figure 3.11: Preserved arenophilic secretion in fossil species of *Pholadomya* (**A-F**) and *Pleuromya* (**G-I**). **A-C**. *Ph. margaritacea*, Barton Bed (Eocene), CAMSM C.56742. **A**. Right view of the specimen. **B**. Detail of a preserved patch of shell material, showing equally distanced lines of arenophilic secretion. **C**. Close up of four fossilised arenophilic lines, evidencing their morphology and sinuous trail on the shell surface. **D-F**. *Pholadomya* sp., Gault (Early Cretaceous). **D**. Preserved arenophilic lines on the central, ribbed portion of the shell (CAMSM B.31776). **E**. Fossilised arenophilic secretion occurring in conjunction with granular ornamentation (CAMSM B.31777). **F**. Preserved secondary threads radiating laterally from the main strand of arenophilic secretion (CAMSM B.31775). **G-I**. *Pleuromya* sp., Swindon Clay (Late Jurassic), CAMSM J.15780. **G**. Right view of the specimen. **H**. Fossilised lines of arenophilic secretion at the ventral shell margin. **I**. Fossilised arenophilic secretion occurring in conjunction with granular ornamentation.

lines of secretion are indeed distinct from other elements of radial ornamentation. While in most specimens only the main strand of secretion has been preserved, a number of arenophilic lines were found in CAMSM B.31775 which displayed secondary threads branching laterally (Fig. 3.11F).

In the sole individual of *Pleuromya* found with fossilised secretion, arenophilic

lines are more or less evenly distributed throughout the preserved surface of the shell (Fig. 3.11G-H). At the margin of the right valve, they were found occurring in conjunction with minute surface granules (Fig. 3.11I).

3.3.2 Mode of preservation

As anomalodesmatan shells are typically rather thin and composed wholly of aragonite their Palaeozoic and Mesozoic fossil record is dominated by internal and external moulds. So at first sight the preservation of arenophilic gland secretions in any fossil material appears highly unlikely. However, the evidence for arenophilic secretions reported here are from specimens collected from organic-rich clay-rich facies which are known to preserve original unstable shell mineralogy and microstructure by hermetically sealing them from dissolution by migrating pore waters (e.g. Kennedy & Hall, 1967; Harper *et al.*, 2002). The very fine nature of the sediment also allows a high fidelity preservation of the external ornament, despite some cracking of the thin shell during compaction. The arenophilic lines themselves appear now to be mineralized and very similar to the shell material. However, it has not been possible to further investigate the replacement of the lines because all specimens bearing fossilised secretion had been extensively lacquered by earlier preparators. It is of note that Aller (1974, p. 55) reporting arenophilic lines in modern *L. norwegica* (which he appears to mistake for spicules) believed them to contain some calcified elements. Although I have not observed these in my material this observation may indicate the ease with which the mucoid secretion may mineralize.

3.4 Phylogenetic considerations

Anomalodesmatans are not the only molluscs capable of covering their periostracum with adventitious particles. The oldest known occurrence of this habit in the phylum is from the Middle Ordovician gastropod *Lytospira norvegica* (reported by Rohr, 1993), and from that time onwards this trait has evolved in numerous other snails. These include not only the marine families Euomphalidae, Turritellidae (Linsley & Yochelson, 1973), Vermetidae (E. A. Kay in Linsley & Yochelson, 1973), Scaliolidae (Ponder, 1994) and Xenophoridae (Morton, 1958), but also one prosobranch and several pulmonate families in the land and freshwater realms (Allgaier, 2007). Among bivalves, capability to incorporate foreign matter is much rarer and has been found outside the

anomalodesmatan clade in only two extant venerid genera, *Samarangia* and *Granicorium*, which Harte (1998) and Taylor *et al.* (1999) consider closely related.

Construction of the extraneous cover in all these molluscs seem to involve either incorporation of debris directly into their calcareous shell, which locally alters the topology of the shell wall and forms an attachment scar (e.g. in xenophorids and euomphalids; see Linsley & Yochelson, 1973), or secretion of adhesive mucus from scattered mucocytes or glands that normally perform a different function (e.g. pallial mucocytes of *Samarangia* and *Granicorium*; see Taylor *et al.*, 1999; salivary and pedal glands of pulmonates; see Allgaier, 2007).

As Prezant (1981*b*) first pointed out, anomalodesmatan arenophilic glands are the only molluscan example of discrete, multicellular organs with a dedicated role in sediment adhesion. However, they are not present in all anomalodesmatans (Table 3.3) and it has remained unclear whether or not these unique organs appeared only once in the evolution of the clade, i.e., if all manifestations of the anomalodesmatan arenophilic system are indeed homologous.

All previous investigators who analysed the glands in detail argued for a single origin of the arenophilic system, gathering it unlikely that such complex organs could have evolved iteratively (e.g. Morton, 1982, 1987*b*; Prezant, 1985*b*). However, both Harper *et al.*'s (2000) morphological dataset and Harper *et al.*'s (2006) mapping of morphological characters over a molecular cladogram favoured two independent origins of arenophilic systems followed by multiple losses, thus prompting a reassessment of their homology.

Primary conjectures of homology are typically based on points of similarity among organisms and their parts, which recognition necessarily entails an element of subjectivity (de Pinna, 1991; Hawkins *et al.*, 1997). Hypotheses so formulated may be subsequently tested by congruence with other characters in analyses of parsimony, but because such a test does not address character analysis and delimitation, it is fundamental that statements of primary homology be testable and potentially refutable based on explicit criteria, namely topological and ontogenetic correspondence, special quality of structures (e.g. shape, size, colour, composition, etc) and function (Rieppel & Kearney, 2002; Agnarsson & Coddington, 2008).

Nothing is currently known of the ontogenetic development of arenophilic systems other than the few fortuitous observations reported in section 3.2.3.1 above. Significantly, however, all other tests of primary homology seem to be fully satisfied by the variety of arenophilic systems found in extant anomalodesmatans. As detailed in section

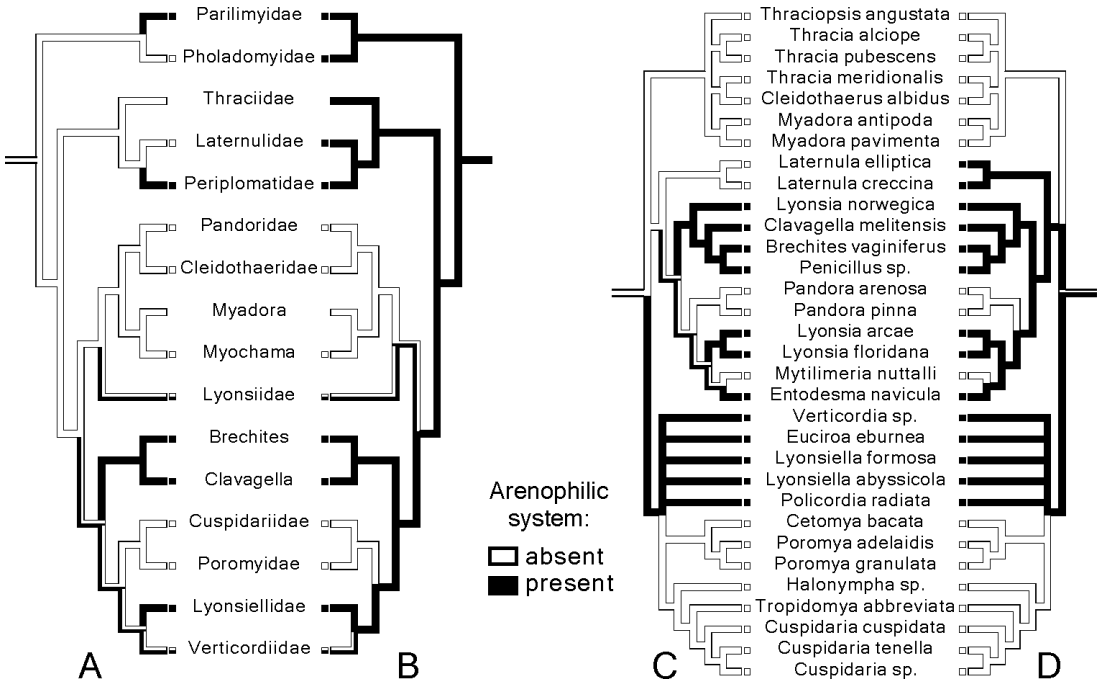


Figure 3.12: Most parcimonious reconstructions of the evolution of anomalodesmatan arenophilic systems on the total evidence morphological tree of Harper *et al.* (2000, fig. 2) (**A-B**) and Maximum Likelihood 18rRNA tree constrained for monophyletic septibranchs of Harper *et al.* (2006, fig. 7) (**C-D**). States attributed to terminal taxa in **A** and **C** are those explicitly coded by Harper *et al.* (2000) and indicated in Harper *et al.* (2006, fig. 7), respectively. In **B** and **D** presence of an arenophilic system was attributed to pholadomyid and laternulid terminal taxa, based on the results of the present study.

3.2.3.3, glands are always positioned internal to and in the vicinity of the periostracal groove, hence fulfilling the topology criterion. They form as invaginations of the pallial ephitelium, comprise at least two kinds of secretory cells divided into core and sheath regions, and discharge virtually identical threads of secretion. Hence, the glands appear to match equally well in special quality, although ultrastructural observations of the glandular cells, which would provide additional tests of this criterion, are currently available only in a few lyonsiids (Prezant, 1981*b*) and are thus uninformative. Finally, all anomalodesmatan arenophilic systems function in the same way, i.e., their adhesive secretion glue extraneous particles to the outside of the periostracal sheet.

Hence, our current knowledge of arenophilic systems and their fine structure does not provide a sound basis to refute the hypothesis of primary homology for different manifestations of the system. Failure to recover a single origin for the glands as the most parsimonious solutions in previous cladistic studies seems attributable to lack

of knowledge of the presence of the organs in some terminals rather than their real absence.

Significantly, when laternulid and pholadomyid taxa included in Harper *et al.*'s (2000; 2006) studies are re-coded as possessing arenophilic glands, based on the results reported herein, homologous glands becomes the shortest optimisation in the morphological cladogram and as parcimonious as convergent alternatives in the molecular tree Fig. 3.12. The hypothesis of homologous arenophilic glands thus withstands the test of congruence with both morphological and molecular datasets.

Table 3.3: Taxa in which an arenophilic system has been recorded or explicitly declared absent. Fossil taxa indicated by †. Only the reference to the first unambiguous record in each species is included, unless subsequent records show disagreement. Anatomical studies that do not mention arenophilic lines or glands in certain taxa were not considered sufficient evidence that these features are absent in those groups.

Taxa	Arenophilic system	Reference and notes
Pleuromyidae		
Pleuromya sp.† (Swindon Clay)	present	Original observations
Pholadomyidae		
Pholadomya candida	absent	Morton (1980)
	present	Original observations
Pholadomya cornueliana†	present	Original observations
Pholadomya margaritacea†	present	Original observations
Pholadomya sp.1† (Gault)	present	Original observations
Pholadomya sp.2† (Lias)	present	Original observations
Parilimyidae		
Parilimya fragilis	present	Morton (1982)
Parilimya maoria	present	Morton (1982), Original observations
Parilimya sp. 1	present	Krylova (2006)
Parilimya sp. 2	present	Krylova (2006)
Parilimya neozelanica	present	Original observations
Thraciidae		
Asthenothaerus maxwelli	absent	Original observations
Parvithracia fragilissima	absent	Original observations
Parvithracia suteri	absent	Original observations
Thracia convexa	absent	Original observations
Thracia meridionalis	absent	Original observations
Thracia phaseolina	absent	Original observations
Thracia similis	absent	Original observations
Thraciopsis angustata	absent	Original observations
Thraciopsis subrecta	absent	Original observations
Trigonothracia jinxingae	absent	Original observations

Periplomatidae		
Cochlodesma praetenue	absent	Prezant (1981*b*)
Offadesma angasi	present	Morton (1981*a*)
Periploma compressum	absent	Original observations
Periploma fragile	absent	Prezant (1981*b*)
Periploma ovatum	absent	Original observations
Pendaloma micans	present	Original observations
Laternulidae		
Laternula boschasina	present	Original observations
Laternula elliptica	present	Original observations
Laternula marilina	present	Original observations
Laternula truncata	absent	Prezant (1981*b*)
	present	Original observations
Pandoridae		
Pandora gouldiana	absent	Prezant (1981*b*)
Lyonsiidae		
Entodesma beana	present	Prezant (1981*b*)
Entodesma chilensis	present	Prezant (1981*b*)
Entodesma cuneata	present	Prezant (1985*a*)
Entodesma fretalis	present	Prezant (1981*b*)
Entodesma inflata	present	Morton (1987*b*)
Entodesma navicula	present	Prezant (1981*b*, as *Entodesma saxicola*)
Entodesma patagonica	present	Prezant (1981*b*)
Lyonsia californica	present	Prezant (1981*b*)
Lyonsia floridana	present	Prezant (1981*b*), Original observations
Lyonsia gouldii	present	Prezant (1981*b*)
Lyonsia hyalina	present	Prezant (1979*a*)
Lyonsia norwegica	present	Original observations
Lyonsia pugetensis	present	Prezant (1981*b*)
Mytilimeria nuttalli	absent	Prezant (1981*b*)
Myochamidae		
Hunkydora novozelandica	absent	Original observations
Myochama anomioides	absent	Harper & Morton (2000)
Cleidothaeridae		
Cleidothaerus albidus	absent	Morton & Harper (2001)
Clavagellidae		
Clavagella australis	present	Morton (1984*a*)
Brechites vaginiferus	present	Morton (1984*b*)
Bryopa aligamenta	absent	Morton (2005)
Dianadema multangularis	present	Morton (2003*a*)
Foegia novaezelandiae	present	Morton (2004*c*)
Humphreyia strangei	present	Morton (2002*b*)
Kendrickiana veitchi	present	Morton (2004*b*)
Nipponoclava gigantea	absent	Morton (2004*a*)
Penicillus philippinensis	absent	Morton (2006*b*)

Verticordiidae		
Laevicordia horrida	absent	Allen & Turner (1974). However, they remark that "Fine sediment usually adheres to the surface of the shell"
Policordia densicostata	present	Allen & Turner (1974)
Policordia atlantica	present	Allen & Turner (1974)
Policordia gemma	present	Allen & Turner (1974)
Policordia insolita	present	Allen & Turner (1974)
Verticordia triangularis	present	Allen & Turner (1974)
Verticordia quadrata	present	Allen & Turner (1974)
Spinosipella deshayesiana	present	Simone & Cunha (2008)
Spinosipella costeminens	present	Simone & Cunha (2008)
Lyonsiellidae		
Lyonsiella abyssicola	present	Allen & Turner (1974)
Lyonsiella subquadrata	absent	Allen & Turner (1974)
Lyonsiella perplexa	absent	Allen & Turner (1974)
Lyonsiella frielei	absent	Allen & Turner (1974) claim arenophilic glands are absent but illustrate fine radiating lines on the valves that are rather suggestive of their presence
Lyonsiella smidti	present	Allen & Turner (1974)
Lyonsiella formosa	absent	Allen & Turner (1974)
Lyonsiella fragilis	present	Allen & Turner (1974)
Lyonsiella compressa	present	Allen & Turner (1974)
Bentholyonsia teramachii	present	Morton (2003*b*)
Cuspidariidae		
Cardiomya cleryana	absent	Original observations
Spheniopsidae		
Grippina californica	absent	Original observations
Spheniopsis frankbernardi	absent	Original observations
Uncertain		
Thracidora arenosa	present	Original observations

Chapter 4

A reappraisal of anomalodesmatan morphological characters

Considering the remarkable ecological and morphological diversity of its extant representatives, it is somewhat surprising that so few comparative studies of the Anomalodesmata have been undertaken. Perhaps due to difficulties in obtaining suitable specimens of an array of component taxa, most anatomical work on the group has been concerned with the functional morphology of single species (e.g. Allen, 1958; Narchi, 1968; Morton, 1982, 2006*b*; Sartori & Domaneschi, 2005).

Comparative treatments of anomalodesmatan morphology have been mostly limited to summaries and discussions of previous work (e.g. Morton, 1981*b*, 1985*a*; Prezant, 1998*b*; Morton, 2007), analyses of a single family or genus (e.g. Prezant, 1981*b*,*c*) or presented as part of larger surveys, often focusing on Bivalvia as a whole (e.g. Ridewood, 1903; Taylor *et al.*, 1973; Purchon, 1987). These efforts culminated in a list of conchological and anatomical features deemed typical of anomalodesmatans (Morton, 1985*a*), which has been used to guide taxonomic decisions and as a source of characters for cladistic analysis (Harper *et al.*, 2000). However, with recent advances in anomalodesmatan systematics, in particular referral of the clade to Heterodonta (see section 1.2.1), many of these morphological features now require re-evaluation (Dreyer *et al.*, 2003; Harper *et al.*, 2006). As Giribet (2008, p. 119) states "Given the major morphological differentiation of this group [Anomalodesmata], despite some homoplasy in many of the characters used to define them, further study of the evolution of the key morphological characters in the light of the seemingly stable molecular results should provide some fascinating insights into their evolutionary relationships".

Two of such "key characters" have been analysed in chapters 2 and 3 above. Dis-

cussing each of the remaining anomalodesmatan organ systems in similar detail would expand this volume beyond reasonable limits. Instead, a brief discussion and reassessment of homology hypotheses for anomalodesmatan morphological features, in particular those listed by Morton (1985*a*) and used in Harper *et al.*'s (2000) cladistic study, is presented here.

This chapter is also intended as a prelude to the novel cladistic analyses of the group presented in chapter 5. Hence, characters formally defined in Appendix C but which have not been previously dealt with in reviews of anomalodesmatan morphology (Morton, 1981*b*, 1985*a*; Prezant, 1998*b*) or used in the cladistic analysis of Harper *et al.* (2000) are also discussed here and cross-referenced in square brackets for convenience.

4.1 Material and methods

Conchological and anatomical characters were studied comparatively in 35 anomalodesmatan taxa listed in Appendix A, which also provides a guide to institutional abbreviations cited in figure captions.

General observations and dissections were carried out under a dissecting microscope with specimens immersed in preservative media (generally 70% ethanol).

For each taxon studied histologically, serial sections were produced of (1) the mantle margins bordering the pedal opening in transverse plane; (2) fused mantle margins between pedal opening and fourth pallial or inhalant apertures in transverse plane; (3) one of the gills in sections perpendicular and parallel to the ctenidial axis; (4) siphons in transverse plane; (5) foot, visceral mass, labial palps and remaining gill in transverse plane. These tissues were dehydrated in a graded ethanol series, treated with xylene and embedded in paraffin wax. The resulting blocks were sectioned at 7 μm and the sections mounted on microscope slides and stained with haematoxylin and eosin.

All material selected for scanning electron microscopy (SEM) was ultrasonically cleaned in distilled water for 20 seconds to 5 minutes depending on the fragility of each specimen, air-dried for 48 hours and gold-coated prior to examination in a JEOL 820 SEM. This included not only whole valves and dissected components (e.g. periostracum) but also shell fractures and etched sections.

Fractures were prepared by placing shells with the desired transect superimposed directly over the sharp edge of a solid object (e.g. a wooden block) and then applying firm pressure to the unsupported portion of the specimen until it broke.

For the preparation of etched sections, specimens were initially air-dried for 48 hours and embedded in polyester resin. After the resin had hardened, material was sectioned along the desired axis using a diamond rock saw. Once cut, cross sections were ground using a series of carborundum powders of decreasing grain sizes, first on a lapidary

wheel (grain sizes of 120 and 60 μm) and then directly on glass plates (grain sizes of 25 and 15 μm). Surfaces were then polished on a lapidary wheel using diamond abrasives of decreasing grain sizes (10, 5 and 3 μm). Finally, sections were etched by immersion in a 0.5% solution of hydrochloric acid for 30 seconds and thoroughly rinsed in distilled water.

4.2 Conchological characters

4.2.1 Shell microstructure [Appendix C, characters 16–17]

Mollusc shells consist of an external, (mainly) organic envelope, the periostracum, and an internal portion of calcium carbonate crystals in an organic matrix (Taylor *et al.*, 1969). The calcified portion is typically divided in layers of different microstructural types, whose identity and arrangement have been considered of phylogenetic significance both in bivalves as a whole (e.g. Taylor, 1973; Carter, 1990) and in anomalodesmatans in particular (Harper *et al.*, 2000, 2006). All shell layers are produced by the mantle, but those secreted at the valve margins are usually divided from those deposited by the proximal portions of the mantle by a layer of myostracal prisms, formed by the pallial epithelium at the line of attachment of the marginal musculature (Fig. 4.1). As noted by Taylor (1973, p. 522) "it is reasonable in most cases to use traces of the pallial myostracum as a marker horizon" when establishing homologies between layers of different taxa.

4.2.1.1 Previously described anomalodesmatan microstructural types

Taylor *et al.* (1973) conducted the most comprehensive (in taxonomic coverage) study of shell microstructure in anomalodesmatans to date and recognised three different arrangements in the group. The first, found in species of *Thracia* and *Cuspidaria*, consisted of a two-layered shell with outer and inner homogeneous layers (Fig. 4.2). The second and third arrangements comprised a three-layered shell with middle and inner nacreous layers, plus an outer layer of either homogeneous or prismatic microstructures, respectively. The second arrangement, with homogeneous outer layer, was recorded only in *Poromya granulata*, whereas the third, a prismato-nacreous shell (Fig. 4.3A–B), occurred in members of all pandoroid and clavagelloid families, in all thracioids but *Thracia*, and in the type species of Pholadomyoidea.

A fourth arrangement was subsequently described by Prezant (1981*c*) in two lyonsiid genera, which consisted of an outer layer of large granules and a nacreous inner layer. Harper *et al.* (2009) recently investigated the large granules in great detail and

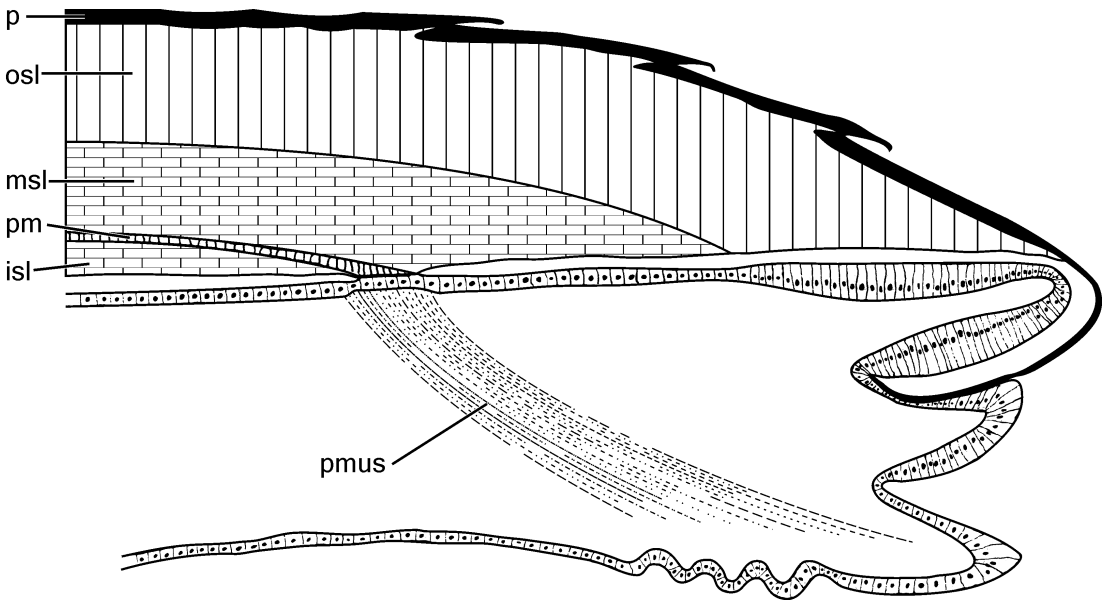


Figure 4.1: Diagram showing the relationship between the anatomy of the mantle and the structure of the shell of *Anodonta cygnea*. Redrawn after Beedham (1958, fig. 1a) and Taylor *et al.* (1969, fig. 1). Abbreviations: **isl**, inner shell layer (nacreous); **msl**, middel shell layer (nacreous); **osl**, outer shell layer (prismatic); **p**, periostracum; **pm**, myostracal prisms; **pmus**, pallial muscles.

showed they are in fact short prisms whose morphology and mode of growth differ from aragonitic prisms deposited by other bivalves.

4.2.1.2 Plesiomorphic arrangement

Among the four arrangements mentioned above, the third, a prismato-nacreous shell, has long been considered to represent the microstructure of the common ancestor of anomalodesmatans, inherited as a plesiomorphic condition. After all, being present in other molluscan groups (e.g. monoplacophorans, archaeogastropods and ammonites) as well as in protobranchs and palaeoheterodonts, such microstructural arrangement has been judged plesiomorphic not only for Anomalodesmata, but for Bivalvia as a whole (Taylor, 1973, p. 522, Prezant, 1998*d*, p. 202, but also see Hedegaard, 1997; Hedegaard & Wenk, 1998).

However, with the recent recognition of Anomalodesmata as a heterodont branch, outgroup analysis indicate that the anomalodesmatan shell may have evolved from an arrangement of crossed-lamellar and complex crossed-lamellar layers, which characterises all other euheterodonts (veneroids and myoids) as well as the next basal branch (Carditoida = Archiheterodonta) (see Fig. 1.6). Any resolution of the euheterodont polytomy with non-monophyletic Veneroida+Myoida would suggest apomorphic gain of

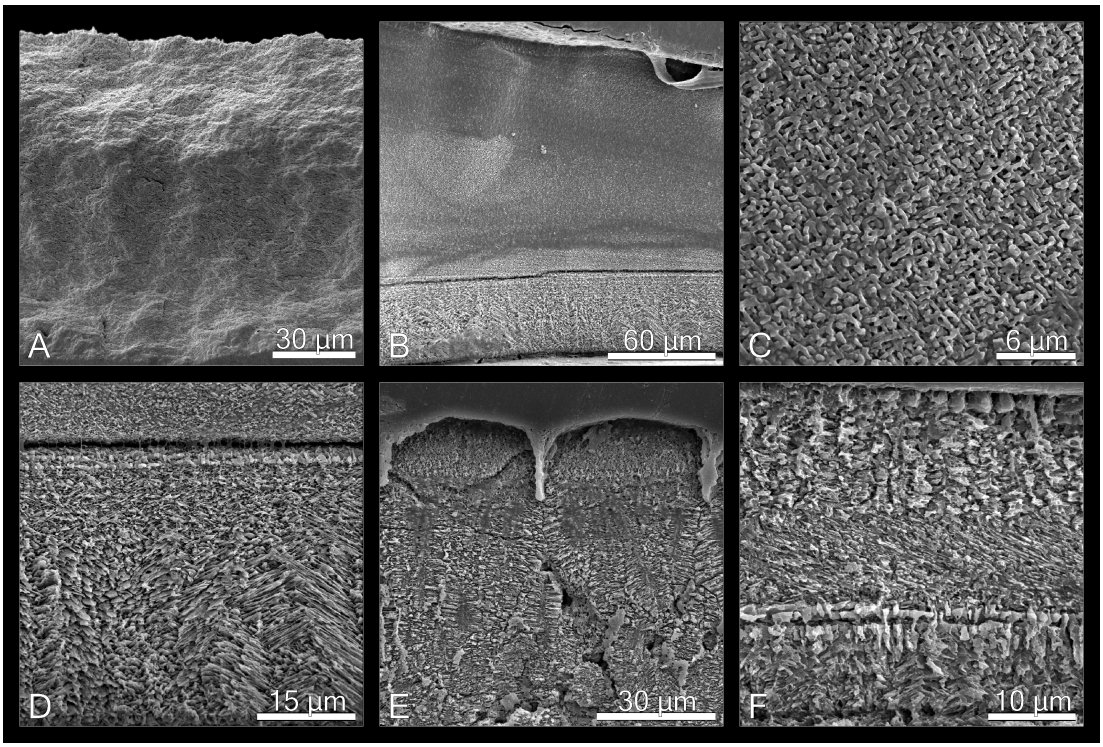


Figure 4.2: Microstructural details of shells traditionally described as homogeneous. External surface towards the top in all subfigures. **A** to **D**. *Cardiomya cleryana*, CENEMAR, unregistered (off Uruguay). **A**. Radial fracture, showing a fine-grained structure in which no pattern can be easily recognised. **B**. Etched radial section, showing three layers of distinct microstructure. **C** and **D**. Details of the middle and inner shell layers shown in **B**, respectively. **E**. *Asthenothaerus maxwelli*, NMNZ M. 183057. Etched radial section showing the outer layer of the shell. **F**. *Parvithracia fragilissima*, NMNZ M. 155144. Etched radial section, showing three layers of distinct microstructure.

the prismato-nacreous shell in Anomalodesmata (from a crossed-lamellar condition) as the most parsimonious solution. With monophyletic Veneroida+Myoida as the sister-group of anomalodesmatans, either the convergent evolution of crossed-lamellar microstructures in Carditoida and Veneroida+Myoida from prismato-nacreous ancestors, or a reversal from crossed-lamellar to prismato-nacreous in Anomalodesmata would require two steps, being thus equally parsimonious solutions.

4.2.1.3 Anomalodesmatan "homogeneous" microstructures

The term homogeneous structure was coined by Bøggild (1930) as a term of convenience for fine-grained structures with no recognisable pattern. As discussed by Taylor *et al.* (1969) and Harper *et al.* (2009), because recognition of patterns depend on the resolu-

tion of the techniques being applied, further and more detailed studies tend to reveal traces of other microstructural types in shells originally described as homogeneous.

The shell of thraciids and cuspidariids has been considered homogeneous throughout and, indeed, no pattern can be recognised in shell fractures of most representatives of these groups (Fig. 4.2A). However, etched sections analysed under scanning electron microscopy reveal patterns which often resemble prismatic and crossed-lamellar microstructures (Fig. 4.2B–F).

Prismatic microstructure comprises parallel, adjacent structural units (first order prisms) which do not strongly interdigitate along their mutual boundaries (Carter & Clark II, 1985; Carter, 1990). Several sub-types of prisms have been defined based on their orientation relative to the shell wall and arrangement of component crystals (second order units). Anomalodesmatan prisms consist of second order units that fan out from a central axis (Fig. 4.3B), being similar in this respect to those of palaeoheterodonts (see Taylor *et al.*, 1969, fig. 17; Checa & Rodriguez-Navarro, 2001).

The outermost portion of the "homogeneous" shell of thraciids and of the cuspidariid *Cardiomya cleryana* often resemble such arrangement, although first and second order elements are much smaller (Fig. 4.2E). It is noteworthy that several anomalodesmatans with a prismato-nacreous shell have prisms that similarly appear homogeneous in most preparations, having often been described as such (e.g. by Aller, 1974 and Baroni *et al.*, 1991). Hence, identification of the outermost layer as prismatic or homogeneous might be, in practice, influenced to some extent by the presence or absence of an underlying nacreous layer and by prior bauplan expectations. Owing to these uncertainties and lack of a marker horizon dividing outer and middle shell layers, I preferred not to define cladistic characters concerned with microstructural variation of the former layer.

In between the outer layer with hints of prismatic structure and the trace of pallial myostracum, most "homogeneous" shells are characterised by tiny acicular elements, arranged obliquely to the depositional surface in two predominant, opposite directions (Fig. 4.2C). This microstructure resemble crossed-lamellar in having crystals arranged in two opposite directions, but differs in that crystals are much smaller and do not form large groups of similar orientation (first order lamels) found in typical crossed-lamellar structure (Fig. 4.3D).

Internal to the trace of pallial myostracum, most thraciid and cuspidariid shells display acicular elements which are coarser than those described above, similarly arranged obliquely to the depositional surface, but displaying numerous distinct orientations as opposed to only two predominant directions (Fig. 4.2D). Such arrangement resembles complex crossed-lamellar structures.

This brief discussion suggests that anomalodesmatan shells typically considered to comprise only two homogeneous layers may in fact consist of three layers of dis-

tinct microstructure. Although traces of prismatic and crossed-lamellar structures were recognised in the studied material, numerous variations of the fine-grained structures described and illustrated herein were found and it was not possible to characterise each of these in detail. A dedicated analysis of these structures, applying more detailed techniques (e.g. TEM, X-ray diffraction; see Harper *et al.*, 2009), is certainly of interest, particularly considering the possibility that anomalodesmatan microstructures might have derived from a predominantly crossed-lamellar shell.

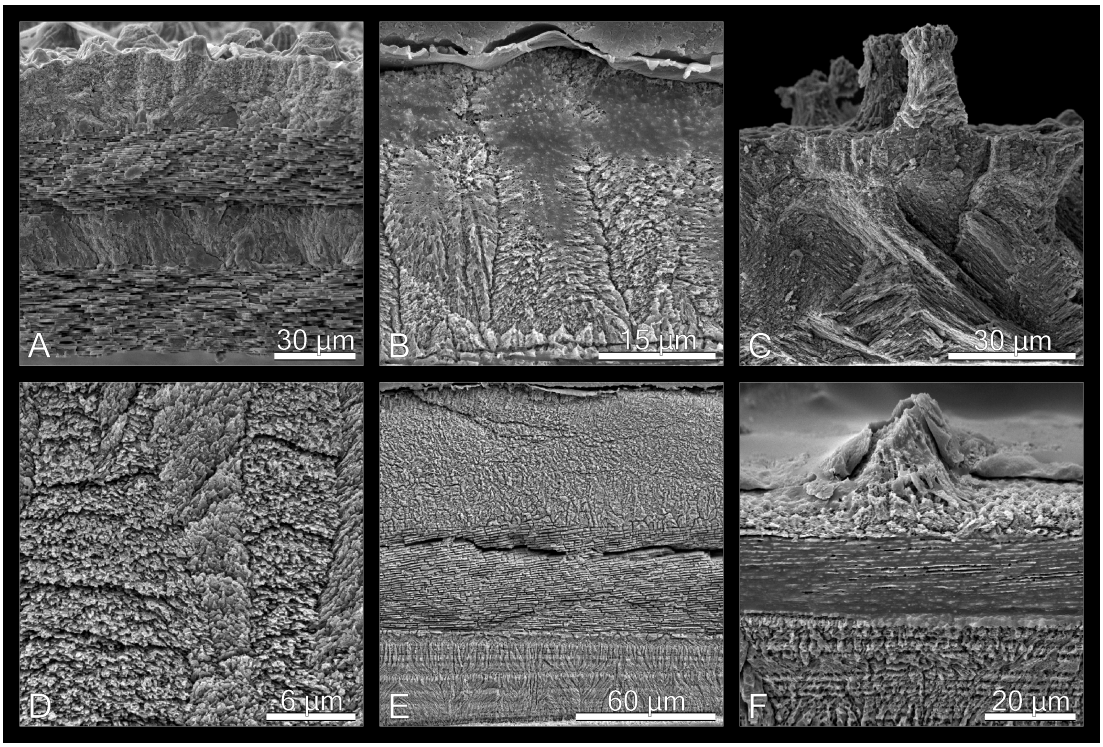


Figure 4.3: Prismato-nacreous shell and microstructural arrangements described for the first time in anomalodesmatans. External surface towards the top in all subfigures. **A** and **B**. *Parilimya neozelanica*, NMNZ M. 183055. **A**. Radial fracture through the right valve. **B**. Etched radial section, showing the outer prismatic layer. **C** and **D**. *Thracidora arenosa*, AMS C447895; 003159B TAS. **C**. Commarginal fracture showing an outer prismatic layer, middle crossed-lammellar layer and calcified periostracal spikes projecting from the external shell surface. **D**. Etched radial section through the crossed-lamellar layer. **E** and **F**. *Thraciopsis angustata* and *Periploma compressum* (MZSP 31378), respectively. Etched radial sections showing three-layered shells with a middle nacreous layer.

4.2.1.4 Novel microstructural arrangements

The present investigation confirmed the presence of previously described microstructural arrangements in several anomalodesmatan families, and revealed two types which

had not been previously reported in the group.

The first, found only in *Thracidora arenosa*, represents the first record of typical crossed-lamellar microstructure in an anomalodesmatan. The crossed-lamellar layer forms the middle sector of the shell wall (Fig. 4.3C), in between a thin outer layer of simple prisms and an inner layer of fine-grained structure, resembling complex crossed-lamellar. The familial allocation of *T. arenosa* is problematic (see Soot-Ryen, 1966; Allen & Turner, 1974) but its anomalodesmatan identity is confirmed by the presence of arenophilic lines on the shell surface, an exclusive feature of the clade.

The second microstructural arrangement is a combination of middle nacreous layer with fine-grained outer and inner layers similar to those of thraciids and cuspidariids, which was found in the periplomatid *Periploma compressum*, myochamid *Hunkydora novozelandica*, and thraciid *Thraciopsis angustata* (Fig. 4.3E, F). Fine-grained structures resembling complex crossed-lamellar were hitherto unknown in periplomatids and myochamids, as was a continuous layer of nacre in extant thraciids.

4.2.2 Calcified periostracal sculpture [Appendix C, characters 5–7]

Numerous anomalodesmatans have the external surface of the shell ornamented by small, discrete elements in the form of granules, spikes or bricks, secreted concomitantly to the periostracal sheet by the inner surface of the outer mantle fold (Aller, 1974). In fact, the elements nucleate and grow within the periostracum and are for this reason commonly referred to as calcified periostracal sculpture (Carter & Aller, 1975). Subsequent accretion of the shell margin (secreted by the outer surface of the outer mantle fold) leads to incorporation of the elements into the outer shell layer.

4.2.2.1 Homology of the elements

Most authors regard all anomalodesmatan calcified periostracal elements as homologous structures (e.g. Morris *et al.*, 1991; Harper *et al.*, 2006), but Harper *et al.* (2000) expressed doubts and preferred not to include characters based on this feature in their cladistic analysis. Although not discussed by the authors, such uncertainty seems to have arisen from (1) the occurrence of similar elements in other bivalves and (2) suggestions of two distinct mechanisms of formation operating in anomalodesmatans.

Extensive periostracal calcification forming elements of ornamentation have been described in several bivalve taxa, including Mytiloida (Carter & Aller, 1975), Gastrochaenidae (Carter, 1978), Veneridae (Ohno, 1996), Cardiidae (Schneider & Carter, 2001) and Lucinidae (Taylor *et al.*, 2004). However, based on significant differences in their morphology and organisation (e.g. in several cases elements are not incorporated into the outer shell layer), as well as their sporadic occurrence within these other bi-

valve grous, these manifestations of periostracal calcification are usually interpreted as independently evolved (but see Carter & Aller, 1975).

Regarding mechanisms of formation, in the methods section of his study on spike production in *Laternula flexuosa*, Aller (1974, p. 43) noted that "spikes in various stages of growth were dissolved out of mantle tissue", a statement which subsequent authors understandably interpreted as evidence that the elements form, at least initially, *within* the mantle. Prezant (1979*b*, p. 94), for example, comments that "Unlike the spinules of *Laternula flexuosa*, another member of the Pandoracea, those of *Lyonsia* are not 'prefabricated' in the mantle (Aller, 1974), but are laid down along with the rather thin periostracum". However, apart from the sentence quoted above, there is little in Aller's (1974) paper that implies the spikes of *L. flexuosa* are produced within the mantle. On the contrary, several passages suggest that they form in association with the periostracum, in the extra pallial space:

> "Spike formation begins on the outer surface of the outer mantle fold, essentially at the line of mantle fusion. Developing spikes are wrapped in a thick periostracum sheet (1.3–3 μ) previously secreted on the inner surface of this fold" (Aller, 1974, p. 45)

> "The tip of a spike is formed first; by analogy with granular layer secretion (Fig. 8 A), the first crystals of ornamentation are probably formed on the inner surface of the periostracum and grow away from it. Subsequent growth proceeds by addition of new fibers in the spike basal section next to the mantle" (Aller, 1974, p. 47)

> "Because of their entrapment between the mantle and the periostracum, the spikes are in effect pushed (simple constraint by the mantle on the base of forming units) into the periostracum during growth" (Aller, 1974, p. 47)

Hence, the mechanism of formation of the spikes of *L. flexuosa* seems identical to that of other anomalodesmatans, but confusion has arisen chiefly due to Aller's (1974) unfortunate choice of words, which merges the mantle living tissue with the periostracal sheet under a single term. A clear example of this amalgamation of terms is provided by the caption to Aller's (1974) figure 3B, a micrograph of the periostracal sheet covering the mantle, which reads "Micrograph of dried mantle surface showing generation of spikes at mantle fusion".

I have not had specimens of *L. flexuosa* available for examination, but failed to retrieve any calcified element from the mantle margins of *L. truncata* after carefully removing the periostracal sheet, ultrasonically cleaning the sample and dissolving it in diluted commercial bleach.

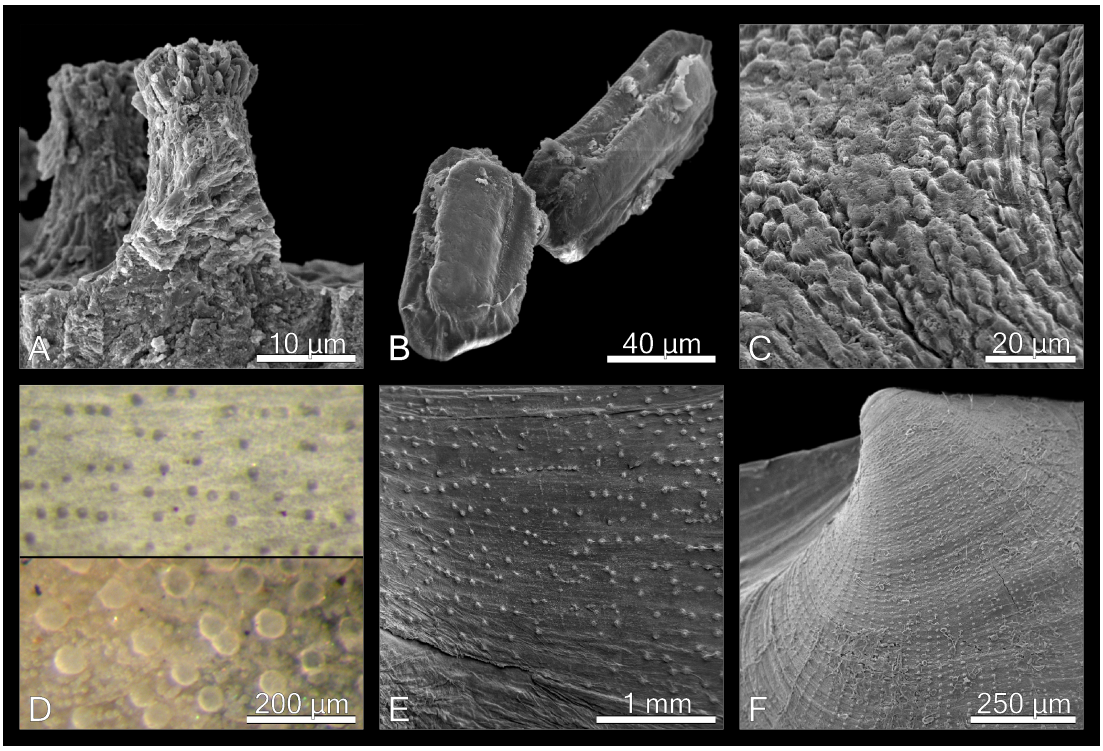


Figure 4.4: Calcified periostracal elements. **A**. *Thracidora arenosa*, AMS C447895. Spicular elements projecting from the external surface of the shell. **B** and **C**. *Hunkydora novozelandica*, NMNZ M. 183056. **B**. Brick-shaped elements extracted from the periostracal sheet by immersion in dilute commercial bleach. **C**. Early portion of the dissoconch, showing granular/spicular elements projecting from its external surface. **D**. *Periploma compressum*, MZSP 44061. Granular elements on the margin of the left valve, anterior (top) and posterior (bottom) to the diagonal ridge. **E**. *Periploma compressum*, MZSP 31378. External surface of the right valve, showing scattered elements without obvious alignment. **F**. *Lyonsia floridana*, FMNH 288890. External surface of the left valve with small spikes organised in neat radial rows.

4.2.2.2 Diversity of form and distribution on the shell wall

Anomalodesmatan calcified periostracal elements may have their longest dimension perpendicular to the shell wall, in which case they project as granules or spikes from the shell surface (Fig. 4.4A), or they may resemble hexagonal bricks or irregular paving stones, having their longest dimension parallel to the shell wall (Fig. 4.4B).

The former type is the commonest among extant anomalodesmatans and the only to have been recorded in Palaeozoic and Mesozoic representatives of the group, the earliest occurrence of spikes in an undisputed anomalodesmatan being from rocks of Ordovician age (in *Rhytimya*; see Pojeta, 1971, pl. 16, fig. 11).

The latter type is characteristic of myochamids, but has also been recorded in a few thraciids (Marshall, 2002). Among taxa analysed herein, those displaying brick-shaped elements as adults also had granules or spikes on the early portions of the dissoconch

(Fig. 4.4C).

Considering brick-shaped elements derived from spikes requires only one transformation in taxa displaying both elements (from spikes to brick-shaped elements in adults), whereas the alternative polarisation requires two transformations (from brick-shaped to spikes both in juveniles of taxa bearing the two types and in taxa bearing only spikes). Hence, the first option should be preferred for being the most parsimonious (generality criterion; ontogenetic method), a decision also supported by the stratigraphic order of appearance of these elements (see Bryant, 2001, for a review and discussion of assumptions of these criteria).

Regardless of their morphology, calcified periostracal elements may be organised in neat radial lines with well-defined interspaces (Fig. 4.4F), or they may lack a clear distribution pattern (Fig. 4.4E). And while in most anomalodesmatans elements are, when present, distributed throughout the dissoconch, in species of *Laternula* and *Lyonsia* they may be either lacking posterior to the diagonal ridge or fading from the umbones to the margin on that portion of the shell surface. Coversely, in several thraciids, periplomatids and myochamids, elements occurring along any particular commarginal band or growth-line are distinctly taller and coarser posterior to the diagonal ridge (Fig. 4.4D).

4.2.3 Hinge teeth [Appendix C, characters 11–15]

Although an edentulous hinge is one of the diagnostic features of Anomalodesmata, a variety of hinge teeth or tooth-like structures are displayed by several representatives of the group. These projections have been traditionally regarded as secondary developments, not homologous with the dentition of other bivalve groups (e.g. Yonge & Morton, 1980). However, with the establishment of Anomalodesmata as an heterodont group (see section 1.2.1), it might be possible to derive anomalodesmatan teeth from the heterodont dentition.

Unfortunately, tracing homologies of the heterodont dentition is by no means an easy task — numerous variations exist and most decisions depend, ultimately, on ontogenetic evidence (Cox *et al.*, 1969; Boyd & Newell, 1969; Evseev *et al.*, 2001, 2004). Because such evidence is rare in anomalodesmatans, there is little option but to use comparisons of the topology, function and special similarity (Rieppel & Kearney, 2002) of adult teeth in establishing hypotheses of primary homology. Harper *et al.* (2000) used the latter criterion to define a single character dealing with dentition, which took into account the relative development of teeth, but not their position. Under such a scheme, taxa bearing a strong tooth anterior to the ligament were attributed the same character state as taxa bearing a similar tooth posterior to the ligament. The difference

in topology in this case is, in my opinion, sufficient to reject the hypothesis of homology between these teeth.

Hence, in comparing anomalodesmatan teeth I distinguished between those occurring in the left and right valves, and took into consideration their position relative to the ligament. Within each subgroup defined as outlined above, an attempt was made to identify teeth as cardinals or laterals using standard criteria — cardinal teeth lie just below the beaks, commonly radiating from the cardinal area, whereas lateral teeth are situated at some distance from the beaks and tend to assume a parallel orientation to the adjacent valve margin (Cox *et al.*, 1969).

A long tooth, parallel to the antero-dorsal margin of the right valve, was recognised in *Thraciopsis angustata* and *Myadora brevis* among taxa analysed herein (Fig. 4.5A) and seems to correspond to a similar tooth described in myochamids (e.g. see Morton, 1977; Harper & Morton, 2000; Marshall, 2002). This tooth is tentatively regarded as homologous to an anterior lateral tooth in the heterodont dentition. Also putatively identified as anterior laterals are the more sharply defined, club-shaped teeth of representatives of the genus *Parvithracia* (Fig. 4.5B) and spheniopsids, studied herein and previously regarded as laterals by Kamenev (2002) and Marshall (2002).

A robust hinge tooth projecting from the hinge plate of the right valve, under the beaks, was found herein only in *Poromya granulata* (Fig. 4.5C), but similar teeth seem to occur in several verticordiids and poromyids (e.g. see Allen & Turner, 1974; Krylova, 2001; Simone & Cunha, 2008). This tooth is tentatively identified as equivalent to the posterior cardinal tooth of the right valve of heterodonts. The feeble projections of the hinge plate of *Pholadomya candida* identified by Runnegar (1972) and Morton (1980), which occupy approximately the same position, were not considered homologous to this tooth not only because they do not interact with the opposite valve, but also because they are rather variable among individuals of that species, and are probably a by-product of absorption of F1 and re-working of the hinge plate (see also section 2.4.2).

A hinge tooth posterior to the ligament of the right valve is present in *Cardiomya cleryana*, *T. angustata*, *Hunkydora novozelandica*, species of *Parvithracia* and spheniopsids (Figs 4.5A, D). Teeth in a similar position are found in several cuspidariids and myochamids (e.g. see Knudsen, 1970; Allen & Morgan, 1981; Morton, 1977; Harper & Morton, 2000; Marshall, 2002). Manifestations of this tooth are rather variable in size and shape but, because only lateral teeth may occur posterior to the ligament in heterodonts, these are tentatively identified as posterior laterals.

No other teeth were identified in material surveyed by the author, but conspicuous projections in the hinge of pandorids and cleidothaerids are noteworthy.

The hinge of pandorids is characterised by several similar, lamelliform teeth that

radiate from the beak in each valve. Boss & Merrill (1965) discussed the hinge of pandorids and showed that the number and disposition of these teeth is highly variable within the family, and that even within species variation of dental configuration may be considerable. Some of these teeth occur posterior to the ligament, a position that is exclusive of lateral teeth in heterodonts, and yet they still radiate from the beaks like cardinals. Due to these peculiarities I concur with most authors in regarding these teeth as secondary structures, to which the term "crura" is commonly applied (Coan *et al.*, 2000; Mikkelsen & Bieler, 2008).

Cleidothaerids display a single tooth in the left valve, which is anterior to the ligament and fits into a matching socket in the cemented right valve (Morton, 1974; Yonge & Morton, 1980). This tooth has been traditionally regarded as secondary but its position and morphology seems compatible with a heterodont cardinal tooth.

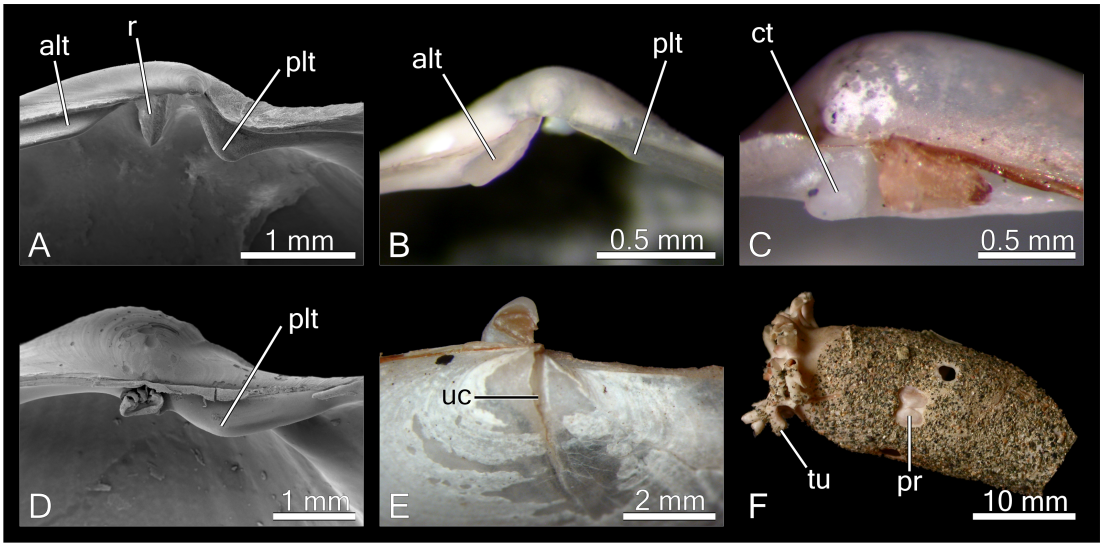


Figure 4.5: **A** to **D**. Lateral view of the hinge of the right valve of *Thraciopsis angustata* (**A**), *Parvithracia fragilissima* (**B**), *Poromya granulata* (**C**) and *Cardiomya cleryana* (**D**), showing several kinds of teeth. **E**. *Periploma ovatum*. External view of the umbo of the left valve, showing a radial slit sealed by repair material. **F**. *Penicillus philippinensis*, BMNH 197637. Dorsal view of the crypt, showing the anterior system of tubules and juvenile shell with both valves fused to the wall of the crypt. Abbreviations: **alt**, anterior lateral tooth; **ct**, cardinal tooth; **plt**, posterior lateral tooth; **pr**, primary (juvenile) shell; **r**, resilifer; **tu**, tubules; **uc**, umbonal slit or crack.

4.2.4 Umbonal slit [Appendix C, character 1]

The umbonal slit (= dorsal or umbonal crack) is a radial fissure through the shell wall, sealed by organic repair material, that extends for a variable distance from the beaks towards the ventral margin (Fig. 4.5E). It first appears in Late Triassic *Cercomya*

(see Runnegar, 1974, pl. 3, fig. 12) and is a diagnostic trait of Periplomatidae and Laternulidae.

The closest bivalve analogue to the fissure seen in these anomalodesmatans is developed in the pteriomorphian endobyssate genus *Pinna*, in which several representatives alter the normal curvature of their shell wall by deforming and breaking previously built portions of the valves (Seilacher, 1984). Elastic material is deposited along the longitudinal keel thus formed, which functions as a hinge, allowing the posterior gape of the shell to be closed against the flexibility of the valves (Chinzei *et al.*, 1982).

In the present study, analyses of growth series of periplomatids and laternulids suggest the fissure appears at about the time of or soon after the onset of growth of the chondrophores that support the fibrous ligament layer F2 (see Figs 2.9 and 2.10). The structure and function of the umbonal slit of laternulids have been investigated by Morton (1976) and Savazzi (1990).

Morton (1976, p. 270–271) considered that the slit increases the flexibility of the valves to compensate for a "relatively ineffective" ligament, which is in some species immobilised by a lithodesma. According to this scenario, the slit would allow adduction of the shell against the flexibility of its wall, which "functions as if it were composed of four valves with an 'external ligament' of fused periostracum".

Savazzi (1990) noticed that the umbones of *Laternula* are less inflated posterior to the slit, where the attachment areas of the ligament are located, than they are anterior to it. He interpreted this as a constraint imposed by the architecture of the ligament apparatus, which would grow excessively if its components, particularly the lithodesma, had to bridge larger distances between the valves.

If the suggestion by Savazzi (1990) that the umbonal slit is a result of constraints to growth imposed by the structure of ligament can stand, then its appearance may be explained by selective pressure for a ligament of that kind, rather than for attributes of the fissure itself.

As explained in section 2.5, evidence from other bivalve groups suggest that anteroposteriorly reduced ligaments supported by chondrophores, such as those of periplomatids and laternulids, are better suited for deep-burrowing than the elongate parivincular ligament that is plesiomorphic for anomalodesmatans. Hence, the umbonal slit might have evolved in association with changes in ligament structure brought about by selective pressure towards deeper-burrowing. Following the appearance of the slit due to growth constraints imposed by the ligament, added flexibility conferred to the shell valves by the fissure (Morton, 1976) may only have aided the rocking movements of the valves about a dorso-ventral axis, for which a ligament supported by chondrophores is adapted (Trueman, 1964; Stanley, 1970; Checa & Cadée, 1997).

4.2.5 Crypt [Appendix C, characters 2–3]

All clavagelloids secrete a crypt (= adventitious tube) but clavagellids and penicillids differ in having either one or both valves fused to its walls and visible from the outside. This difference has led to much debate about whether or not these structures are homologous (e.g. Savazzi, 1982, 1999, 2000, 2005; Morton, 2005, 2006*a*,*b*, 2007).

Harper *et al.* (2000) coded both crypt types under their character 42 (ability to build calcareous tubes: absent/present), thus implying homology between these morphologies. Their analysis recovered monophyletic Clavagelloidea, as did the molecular tree of Harper *et al.* (2006).

In spite of these results, Morton (2007, p. 58) has recently argued that Clavagellidae and Penicillidae independently evolved from ancestors similar to extant lyonsiids, so that their "infaunal tube building and the cemented watering pot lifestyles have both evolved independently in the two families at different times, and thus constitute two remarkable examples of convergent evolution".

In my view, two shared features of clavagellid and penicillid crypts strongly suggest that they represent homologous structures, as envisaged by most authors.

First, in both taxa at least the left valve is fused to the wall of the crypt and visible from the outside. Although the tube-dwelling life habit has evolved independently in two other bivalve lineages (Grastrochaenidae and Pholadoidea), only in clavagelloids is the shell fused to the wall of the crypt (Carter, 1978; Savazzi, 1999).

Second, both clavagellids and penicillids, with the possible exception of *Bryopa* (see Savazzi, 2000), secrete a system of open tubules at the anterior end of the crypt, often termed watering pot (Fig. 4.5F), which is unknown in other tube-dwellers (compare, for example, the photographs of tubules in representatives of both groups, reproduced by Smith, 1976).

If all manifestations of the clavagelloid crypt are indeed homologous, one may ask which represents the plesiomorphic mode of formation of the structure: being secreted by the left mantle lobe alone (resulting in a left valve fused to its wall), or by both mantle lobes (i.e. with both valves visible from the outside). Intermediate morphologies are not feasible (Savazzi, 1982) and sampling of clavagelloids in cladistic studies has thus far proved insufficient to favour one possibility or the other. Hence, the only clue to this query is stratigraphic order, with the first known appearance of the former condition (left valve fused) dating from the Late Cretaceous, and that of the latter morphology (both valves fused) from much later, in the Early Oligocene (Smith, 1962*a*). However, bearing in mind the scarce and patchy fossil record of clavagelloids (Smith, 1962*a*; Savazzi, 2000), stratigraphic evidence should be interpreted with caution.

4.2.6 Cementation [Appendix C, character 4]

Among anomalodesmatans, cementation occurs in cleidothaerids, some myochamids, some clavagellids and in the penicillid genus *Humphreyia*. Ability to cement was coded as a single character by Harper *et al.* (2000, character 41), implying homology of all its manifestations.

Nevertheless, while representatives of the former three families attach to hard substrata via the shell valves, in *Humphreyia* it is the wall of the crypt, not the bivalved shell, that is cemented. In fact, most endobenthic clavagelloids have clasts cemented to the crypt wall (Fig. 4.5F; Harper & Morton, 2004, fig. 2; Savazzi, 2005, fig. 5), and Morton (2002*a*) recorded several individuals of *Brechites vaginiferus* (a penicillid that normally lives burrowed in soft sediments) cemented into rock crevices. This trait seems related to the mechanism of secretion of the crypt (Harper & Morton, 2004) and is therefore not homologous to cementation by the valves.

The remaining taxa cement via the shell valves, but clavagellids have the left valve attached to the wall of the borehole, whereas both cleidothaerids and myochamids cement via the right valve (Harper & Morton, 2000; Morton & Harper, 2001).

4.3 Mantle and siphons

4.3.1 Mantle fusion and fourth pallial aperture [Appendix C, characters 18, 19, 21, 25]

The union of right and left mantle margins has long been recognised as an important step in bivalve evolution, not only for providing an effective way of separating inhalant and exhalant water currents, but also for representing a first step towards the development of siphons and a better control of water pressure in the pallial cavity, both fundamental for the radiation of bivalves into the infaunal realm (Trueman, 1954; Yonge, 1957, 1982, 1983; Stanley, 1969).

Connection between the mantle lobes may occur only between inhalant and exhalant openings, or also delimit up to three openings into the infra-branchial chamber, namely inhalant, pedal and fourth pallial apertures (Atkins, 1937*a*; Yonge, 1957). In all anomalodesmatans, mantle fusion delimits exhalant, inhalant and pedal openings, and in several a tiny forth pallial aperture is present between the latter two (Fig. 4.6). Behavioural and anatomical analyses of living specimens have hitherto failed to reveal the function of this tiny additional aperture in anomalodesmatans (see Sartori & Domaneschi, 2005, for a review) but in other bivalves pseudofaeces have been observed being expelled by an analogous opening (Atkins, 1937*a*; Yonge, 1948*b*).

Across the Bivalvia, the nature of connection between mantle lobes may be ciliary, cuticular or tecidual. Only the last type occurs in anomalodesmatans, but there are significant differences in the extent of pallial epithelium involved in the union.

The bivalve mantle margin is thrown into folds, the commonest condition being the presence of three of such divisions, an outer fold in between the calcified portion of the shell and the periostracum, and middle and inner folds positioned internal to the periostracal groove (Fig. 4.1). Yonge (1957) noticed that fusion of the mantle lobes could be accomplished by the inner folds alone or also involve the middle folds either partially or completely. These three degrees of fusion have been widely used for comparisons across taxa in both authoritative and cladistic studies, including that of Harper *et al.* (2000, character 13).

However, there are numerous variations in the arrangement of the bivalve mantle margins, both in the number of folds and in their morphology and function. Arcoids, for example, have two folds in between calcified shell and periostracum and most display a single fold internal to the periostracal groove (Oliver & Holmes, 2006, table 1), whereas in venerids three marginal folds are present in the latter position (Hillman & Shuster Jr, 1966; Sartori *et al.*, 2008). Hence, establishing homologies among folds may be problematic when comparing representatives of different families and superfamilies. As noted by Waller (1978, p. 345) "the only clearly homologous structure between major groups is the periostracal groove itself".

These intrinsic difficulties in the recognition of homologous folds may be exacerbated by artefacts of preservation, a problem that is particularly serious when histological sections are only available from single individuals whose curation history is unknown, as is commonly the case in studies of anomalodesmatans (e.g. most taxa analysed herein; Morton, 1980, 1982, 2005).

Due to these uncertainties, I preferred to take only the periostracal grooves as homologous and compare the following two attributes across taxa: (1) absence or presence of a continuous periostracal sheet covering the pallial margins, which indicates fusion of left and right periostracal grooves; and (2) if a continuous periostracal sheet is absent, whether the fused portion between left and right periostracal grooves is narrow or very wide.

Fusion of the periostracal grooves corresponds to Yonge's type C fusion and, within Anomalodesmata, occurs ventrally only in clavagelloids, where it constitutes a prerequisite for the deposition of the crypt (Harper & Morton, 2004). It also occurs in the formation of siphons of laternulids and clavagelloids, so that in both taxa the siphonal tubes are enveloped in periostracum, except at their distal apertures (Fig. 3.1).

Among taxa investigated herein, only *Pholadomya candida* and *Parilimya neozelanica* have a wide mantle margin in between left and right periostracal grooves, all

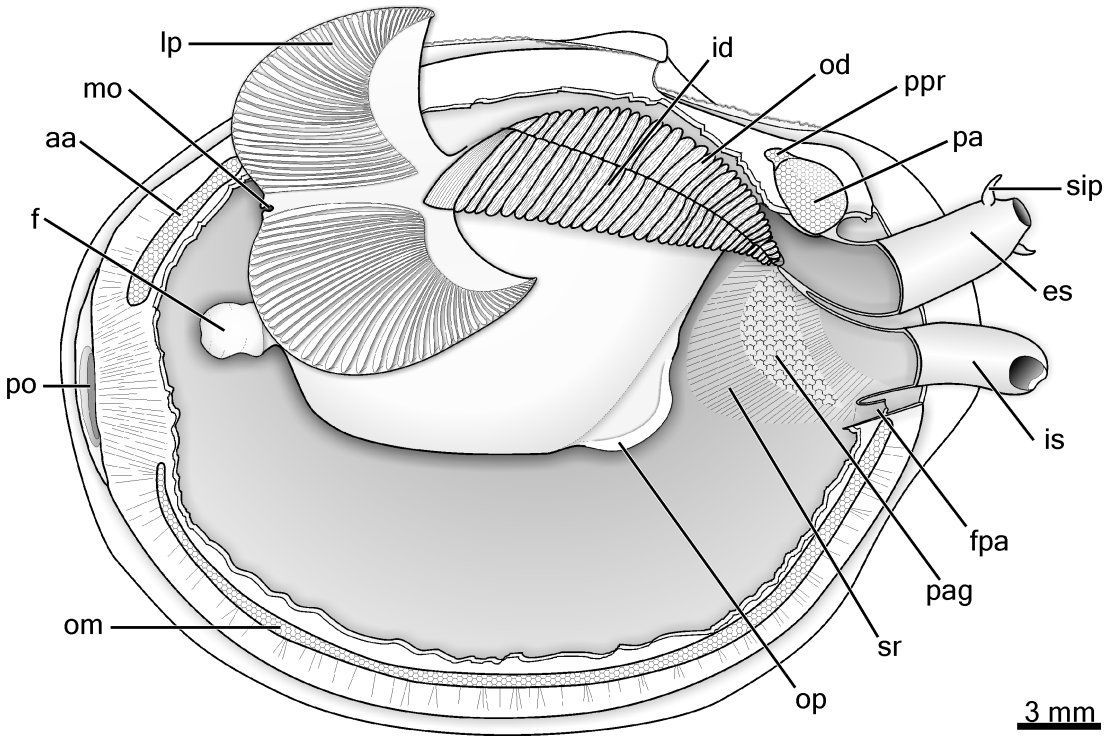


Figure 4.6: *Periploma compressum*, CENEMAR unregistered. Diagram of a dissected specimen in left view, showing the organs of the pallial cavity. Abbreviations: **aa**, anterior adductor; **es**, exhalant siphon; **f**, foot; **fpa**, fourth pallial aperture; **id**, inner demibranch; **is**, inhalant siphon; **lp**, labial palp; **mo**, mouth; **od**, outer demibranch; **om**, orbital muscle; **op**, opisthopodium; **pag**, pallial gland; **pa**, posterior adductor; **po**, pedal opening; **ppr**, posterior pedal retractor; **sip**, siphonal papilla; **sr**, siphonal retractor.

other surveyed species displaying only a narrow crest in that position (Fig. 4.7A–D).

4.3.2 Pigmentation [Appendix C, character 24]

The mantle and siphons of anomalodesmatans may be completely devoid of pigmentation or they may bear pigmented areas, specially around inhalant and exhalant apertures. For almost all taxa analysed herein only preserved specimens were available and hence the possibility of artefactual absence of some pigments in the material cannot be dismissed. Dark brown and black areas, as well as sub-epithelial granules of pigment in histological sections (Fig. 4.7E), were found only in laternulids, lyonsiids and *Pholadomya candida*. Additionally, literature accounts record the presence of pigments in the mantle and/or siphons of clavagelloids, pandorids, cleidothaerids and poromyids (Hancock, 1853*a*; Boss & Merrill, 1965; Morton, 1984*a*, 1981*c*, 2002*a*).

4.3.3 Pallial glands [Appendix C, character 23]

Other than arenophilic glands, discussed in detail in chapter 3, the mantle of anomalodesmatans may display glandular areas of varying cytological aspect. Some of these areas have been recorded only in individual species so far, such as the large sub-epithelial gland positioned just posterior to the pedal opening of *Bentholyonsia teramachii* (Morton, 2003*b*, fig. 8). In thraciids, periplomatids, myochamids and juvenile *Cleidothaerus albidus* part of the internal epithelium of the right mantle lobe is glandular (this study; Morton & Harper, 2001), with tall, columnar cells carrying eosinophilic secretory globules (Figs 4.6, 4.7F). The function of this gland is unknown. In *Cleidothaerus albidus*, a species that ceases to cement during its ontogeny, Morton & Harper (2001) found the glands in juveniles but not in adults and, based on this observation, suggested that they may be the source of cement. Sartori & Domaneschi (2005) indicated that the glands of *Thracia meridionalis* secrete mucus for agglutination of pseudofaeces.

4.3.4 Pallial muscles [Appendix C, characters 8, 20]

The bivalve mantle margins are retracted by bundles of muscle fibres attached to the shell wall (Fig. 4.1). Neighbouring attachment points are approximately equidistant from the edge of the valves and hence an impressed line is formed on the internal surface of each valve (pallial line). This line is usually continuous, but in some taxa bundles of fibres may come together and form independent attachment scars separated by interspaces. Among anomalodesmatans, the latter condition is only known in pandorids (Boss & Merrill, 1965).

Along fused sectors of the mantle, bundles of muscle fibres attaching to one of the valves may cross the mid sagittal point of fusion and penetrate the opposite mantle lobe. Groups of crossing fibres generally retain a dedicated function in pallial retraction and an oblique orientation to the internal surface of the shell (Fig. 4.8A). However, in some taxa, including pholadomyoids, periplomatids and laternulids, the pallial musculature is hypertrophied and attach to both valves in an approximately perpendicular orientation (Fig. 4.8B). These hypertrophied fibres, termed orbital muscles by Morton (1973*a*), function primarily in shell adduction.

4.3.5 Siphonal retractors [Appendix C, character 29]

Siphonal tubes are elaborations of the mantle margins and it is hence unsurprising that their retraction is effected by pallial muscles whose degree of development is associated to the length of the siphons. Siphonal retractors generally resemble the other sectors of pallial musculature in that individual bundles of fibres are approximately equal in size and attach side by side along a line on the internal surface of the shell (pallial sinus).

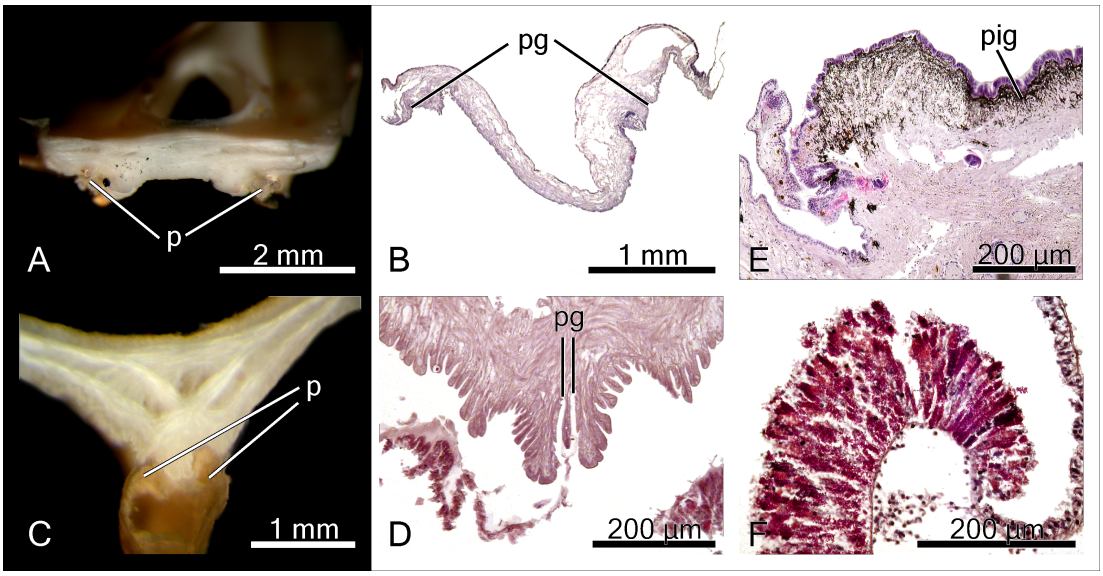


Figure 4.7: Mantle fusion and other pallial characters. **A** to **D**. General and histological aspects of transverse sections through the ventral mantle margin of *Parilimya neozelanica* (**A** and **B**; NMNZ M. 183055. 2004030) and *Asthenothaerus maxwelli* (**C** and **D**; NMNZ M. 183057). **E**. *Laternula truncata*. Longitudinal section through the dorsal wall of the exhalant siphon, showing densely distributed, sub-epithelial granules of dark pigment. Distal tip of the siphon towards the left-hand side. **F**. *Hunkydora novozelandica*, NMNZ M. 183056. 2004030. Transversal section through the right mantle lobe, showing a pallial gland comprising high columnar cells filled by globules of secretion. Dorsum towards the top. Abbreviations: **p**, periostracum; **pig**, pigment granules; **pg**, periostracal groove.

However, that is not the case in parilimyids and some lyonsiellids, whose siphons are connected not only to the pallial sinus by relatively short and feeble fibres, but also to a round scar in the anterior half of the shell by a pair of massive bundles of muscle fibres (Fig. 4.8E; Allen & Turner, 1974; Morton, 1982, 1984*c*, 2003*b*). A presumably intermediate condition between typical bivalve siphonal retractors and the immense bundles described above is seen in *Pholadomya candida*, which has a pair of hypertrophied muscular bundles inserted in the pallial sinus among the remaining siphonal retractor fibres (Fig. 4.8F). Owen (see Morton, 1980, appendix 1) referred to this pair of enlarged bundles as "taenioid internal retractors" and Morton (1982, 1984*c*, 2003*b*) adopted and extended use of the term to any hypertrophied muscle connected to the siphons.

While in *P. candida*, parilimyids and *Lyonsiella fragilis* taenioid muscles are separated from the ventral mantle margins (Allen & Turner, 1974; Morton, 1982), in *Lyonsiella formosa* and *Bentholyonsia teramachii* they run along that margin (Morton, 1984*c*, 2003*b*). Although this difference in topology may suggest two non-homologous types of hypertrophied siphonal retractors, having not examined specimens of Lyonsiel-

lidae and with only cursory descriptions of these organs in representatives of the family available in the literature, I have followed Morton (2003*b*) in regarding all taenioid muscles homologous.

4.3.6 Histology of the siphonal walls [Appendix C, characters 31–32]

Studies of the histology of the siphonal walls have been undertaken in numerous bivalves, either in detailed investigations dealing with single species or comparatively (e.g. Ansell, 1961; Duval, 1963; Fishelson, 2000). These surveys revealed that siphonal walls typically consist of strong longitudinal muscles which form the bulk of the organ and are bounded both externally and internally by layers of circular musculature. In addition to these elements, radial muscular fibres link outer and inner epithelia.

The longitudinal muscles of the siphons are divided into outer and inner blocks by a central hemocoel and often by an additional central band of circular musculature (Fig. 4.8C, D; Duval, 1963). Among anomalodesmatans, this central layer of circular musculature was recorded in laternulids, lyonsiids, clavagelloids and *P. candida* (this study; Morton, 1980, 1984*b*), but is absent in parilimyids, cuspidariids, thraciids, myochamids, periplomatids and cleidothaerids (this study; Morton, 1974, 1982; Allen, 1958; Sartori & Domaneschi, 2005)

Nerve cords running along the siphons of anomalodesmatans may occupy the central hemocoel or they may be embedded in the inner block of longitudinal muscles (Fig. 4.8C, D). Nerves occupy the former position in cuspidariids, thraciids, myochamids and some periplomatids (this study; Allen, 1958), and the latter position in pholadomyoids, laternulids, lyonsiids and clavagelloids (this study; Morton, 1980, 1984*a*,*b*).

4.3.7 Mucus-lined siphonal passages [Appendix C, character 30]

The siphons of at least some thraciids and periplomatids are known to form mucus-lined galleries through the sediment, a trait that is probably unique among bivalves (Yonge, 1937; Morton, 1981*a*; Sartori & Domaneschi, 2005). Once the mucus lining is completed, the siphonal tips are partially withdrawn and the animal may move deeper into the sediment (Yonge, 1937; Sartori & Domaneschi, 2005). This behaviour presumably reduces the risk of predation, particularly siphonal nipping by fish (Peterson & Quammen, 1982).

4.3.8 Tentacles and sense organs [Appendix C, characters 26–27]

Tentacles surrounding inhalant and exhalant apertures are present in most suspension-feeding bivalves, where they may curve inwards to act as strainers (Narchi & Dario, 2002) or bear a primarily sensorial function, in which case they may display sense

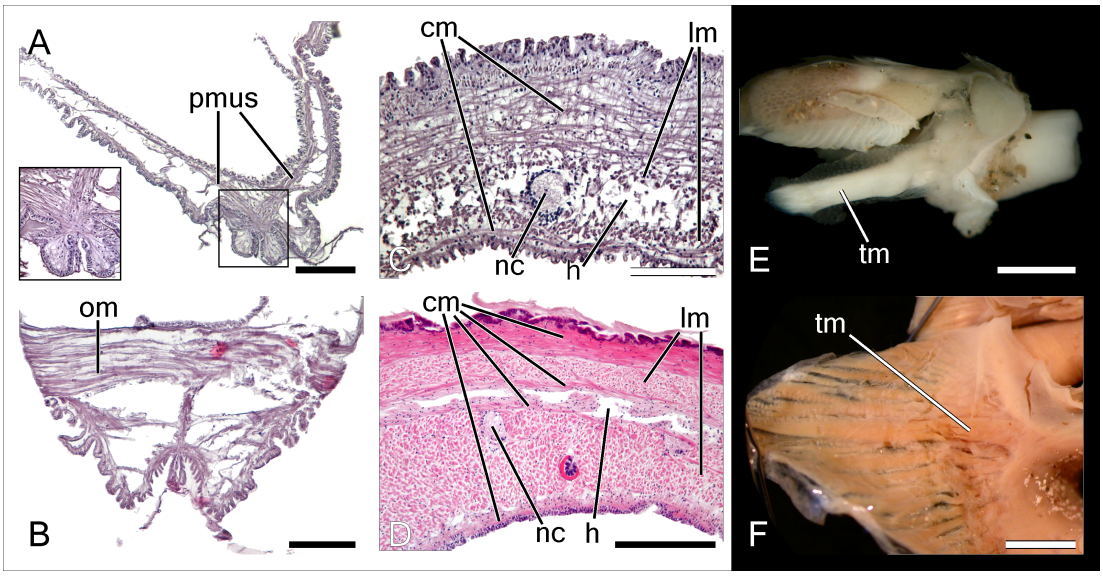


Figure 4.8: Pallial musculature. **A** and **B**. Transversal sections through the ventral mantle margin of *Hunkydora novozelandica* (NMNZ M. 183056. 2004030) and *Periploma compressum* (MZSP 31378), respectively, showing the orientation of the pallial muscles. **C** and **D**. Transversal sections through the siphonal walls of *Hunkydora novozelandica* (NMNZ M. 183056. 2004030) and *Laternula boschasina*, respectively, showing the organisation of circular and longitudinal muscle layers and position of nerve cords. **E**. *Parilimya neozelanica*, NMNZ M. 183055. 2004030. Left view of a dissected specimen, showing a hypertrophied muscular bundle extending further anteriorly than the remaining siphonal retractors. **F**. *Pholadomya candida*, ZMUC unregistered. Internal view of the siphonal region, showing a hypertrophied muscular bundle among the remaining siphonal retractors of the right mantle lobe. Abbreviations: **cm**, circular musculature; **h**, hemocoel; **lm**, longitudinal musculature; **nc**, nerve cord; **om**, orbital muscle; **pmus**, pallial muscles; **tm**, taenioid muscle. Scale bars: **A** = 250 μm; **B** = 250 μm; **C** = 150 μm; **D** = 200 μm; **E** = 3 mm; **F** = 5 mm.

organs not seen elsewhere along the mantle margins (Adal & Morton, 1973; Hodgson & Fielden, 1984, 1986).

Laternulids, lyonsiids, pandorids and clavagelloids have conspicuous tentacles, normally organised in two or more rows around the siphonal apertures (Figs 3.3, 4.9A–C), and with a terminal ciliated pit that resembles type III sense receptors described by Hodgson & Fielden (1984). Observations of living specimens of some of these taxa have recorded sensitivity of the siphons to mechanical and light stimulation (Morton, 1973*a*; Narchi, 1968; Thomas, 1994). In species of *Laternula*, tentacles of the outermost ring bear a complex eye at their distal tip (Fig. 4.9F), which comprises a pigment cup, retina and lens, among other elements (Adal & Morton, 1973). Simpler photoreceptors might be present in some lyonsiids (Prezant, 1984, conference abstract), but none were found in *Lyonsia floridana* or *L. norwegica*, analysed herein.

Although the siphonal walls of most septibranchs are devoid of appendages, long

tentacles project from the mantle margins around inhalant and exhalant apertures (Fig. 4.10). These tentacles bear ciliated sense organs at their apical tips and are thought to function in the detection of prey (Reid & Crosby, 1980; Morton, 1987*a*; Krylova, 2001). I have tentatively considered all pallial appendages with a ciliated apical pit to be homologous structures.

The mantle margins of the remaining anomalodesmatans are either devoid of appendages (e.g. in pholadomyoids) or they may bear few, rather short papillae, normally organised in a single ring around the inhalant and/or exhalant apertures, and devoid of an apical ciliated pit (Fig. 4.9D, E). These papillae may, however, concentrate smaller and simpler sense organs (type I of Hodgson & Fielden, 1984, 1986), also found elsewhere on the siphonal walls, which are difficult to observe in "conventional" histological sections (wax embedded, stained in haematoxylin and eosin). Using scanning electron microscopy, Sartori & Domaneschi (2005) revealed the presence of these receptors in *Thracia meridionalis*, whose siphons are almost insensitive both to mechanical and photic stimulation.

4.3.9 Siphonal cowl [Appendix C, character 28]

Bivalve siphons are usually cylindrical or conical projections of the mantle margins, with dorsal and ventral walls approximately equal in length and distal aperture facing posteriorly. This is not the case in poromyids and lyonsiellids, whose dorsal wall of the inhalant siphon projects further than the ventral, directing the distal aperture ventrally (Fig. 4.9G). Morton (1981*c*, 1984*c*, 1987*a*) interpreted this morphology, which resembles a cowl, as an adaptation to capture benthic prey after observing *Poromya granulata* burrowing at an angle of approximately 45° with the ventral margin of the shell downwards.

4.4 Gills and labial palps

4.4.1 Nature and alignment of the gills [Appendix C, characters 33–35]

The commonest configuration of the gills of bivalves is a pair of filamentous ctenidia largely concerned with the collection of food particles during filter-feeding. This type of gill, which primitively consists of a central axis with one V-shaped series of filaments projecting from its left and one from its right side, has been widely modified across the Bivalvia (see Ridewood, 1903; Atkins, 1937*b*), at times by the loss of one of the V-shaped series (a demibranch) or, more commonly, of only one arm of the V (a lamella).

All filter-feeding Anomalodesmata are characterised by ctenidia with a complete inner demibranch in between the axis and the body wall, and an outer demibranch comprising only one lamella (type E of Atkins, 1937*b*).

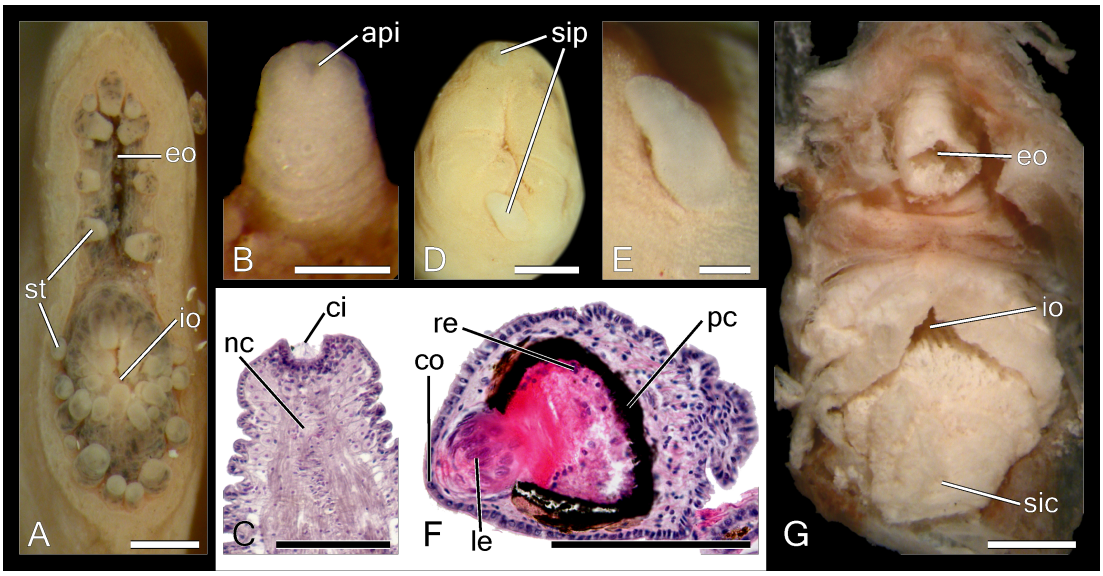


Figure 4.9: Sense organs and other structures associated with the siphons of anomalodesmatans. **A** to **C**. *Lyonsia norwegica*. **A**. External view of the siphons, showing multiple rows of tentacles around the distal apertures (BMNH 20070070). **B**. Detail of a tentacle surrounding the exhalant aperture, showing its apical pit (BMNH, "Sarsia" cruise stn. no. 360A). **C**. Longitudinal section through a tentacle, showing long cilia in the apical pit and a thick nerve cord running along the length of the tentacle (BMNH 20070070). **D** and **E**. *Periploma compressum*, CENEMAR unregistered. **D**. External view of the distal tip of the exhalant siphon, showing two papillae bordering the aperture. **E**. Detail of a papilla. **F**. *Laternula boschasina*. Longitudinal section through a siphonal tentacle, showing a complex photoreceptor at its distal tip. **G**. *Bentholyonsia* sp., NMNZ TAN0707/73, Challenger Plateau 30350. Internal view of the posterior mantle margin, showing the siphons withdrawn into the pallial cavity and the siphonal cowl of the inhalant siphon. Abbreviations: **api**, apical pit; **ci**, cilia; **co**, cornea; **eo**, exhalant opening; **io**, inhalant opening; **le**, lens; **nc**, nerve cord; **pc**, pigment cup; **re**, retina; **sic**, siphonal cowl; **sip**, siphonal papilla; **st**, siphonal tentacle. Scale bars: **A** = 0.5 mm; **B** = 0.2 mm; **C** = 0.1 mm; **D** = 1 mm; **E** = 0.25 mm; **F** = 0.1 mm; **G** = 1 mm.

However, in the carnivorous families Cuspidariidae and Poromyidae the gills are largely modified into a muscular membrane (septum) with filaments either completely lacking or restricted to small areas. In taxa lacking ctenidial filaments (Fig. 4.10), the septum is only perforated by slit-like apertures (ostia) and cilia are restricted to the borders of these apertures (Ridewood, 1903; Yonge, 1928).

While most authors regard ctenidia and septum homologous structures, the alternative view that the latter represents a new structure which succeeded the obliteration of the ctenidia has been intensively debated and is yet to be unequivocally dismissed (e.g. Dall, 1886*a*,*b*, 1889*b*; Pelseneer, 1888*a*,*b*, 1889, 1891*a*; Ridewood, 1903; Yonge, 1928; Bernard, 1974; Allen & Turner, 1974; Allen & Morgan, 1981).

Favouring a ctenidial origin but considering it unlikely that the septum could be derived from gills specialised in suspension feeding, Purchon (1963) hypothesised cus-

pidariids and poromyids evolved from bivalves bearing ctenidia with an exclusively respiratory function, similar to those of extant protobranchs. This argument has influenced removals of these families from Anomalodesmata and referral to either other bivalve higher groups (e.g. by Runnegar, 1974; Bernard, 1974) or erection of a subclass of their own (e.g. by Nevesskaja, 2009). However, these ideas should no longer be entertained since it is now clear that all septibranch families belong to Anomalodesmata (von Salvini-Plawen & Steiner, 1996; Giribet & Wheeler, 2002; Dreyer *et al.*, 2003; Harper *et al.*, 2006).

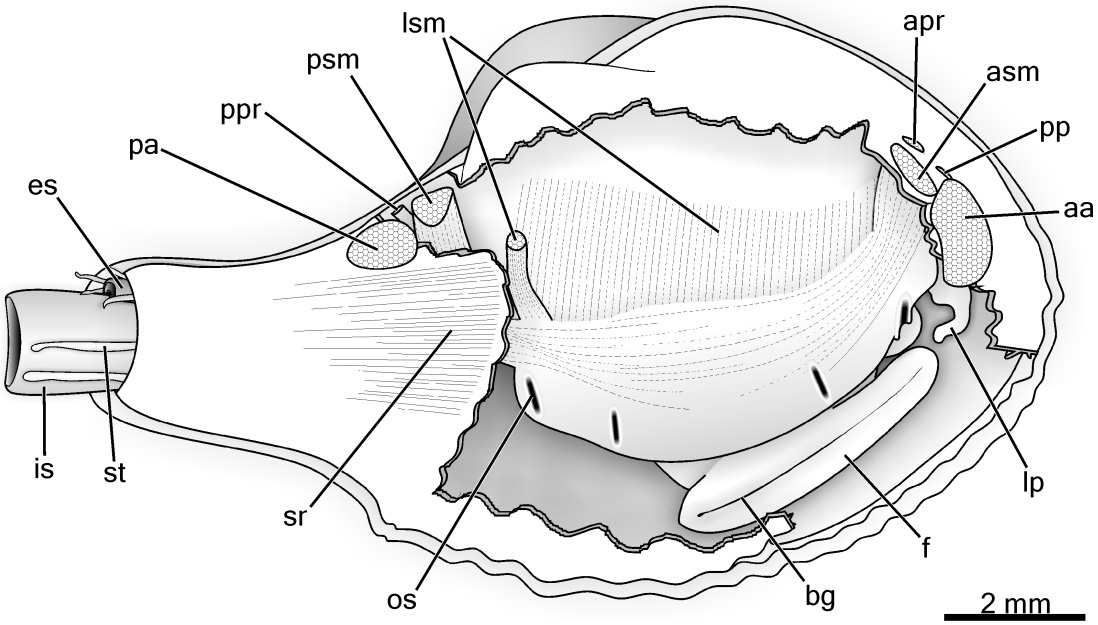


Figure 4.10: *Periploma compressum*, CENEMAR unregistered (Santos, SP, to São Francisco do Sul, SC, Brazil). Diagram of a dissected specimen in right view, showing the organs of the pallial cavity. Abbreviations: **aa**, anterior adductor; **apr**, anterior pedal retractor; **asm**, anterior septal muscle; **bg**, byssal groove; **es**, exhalant siphon; **f**, foot; **is**, inhalant siphon; **lp**, labial palp; **lsm**, lateral septal muscles; **os**, ostium; **pa**, posterior adductor; **pp**, pedal protractor; **ppr**, posterior pedal retractor; **psm**, posterior septal muscle; **sr**, siphonal retractor; **st**, siphonal tentacle.

Most anomalodesmatans with type E ctenidia have the gills aligned dorso-ventrally. In these forms the outer demibranch runs from the ctenidial axis towards the dorsum, and the inner demibranch is directed ventrally, with its two lamellae approximately parallel to one another (Fig. 4.11B).

Nonetheless, in a few taxa with type E ctenidia and in those bearing muscular septa, the gills are perpendicular or nearly so to the mid-sagittal plane of the body, forming a horizontal division between infra and supra-branchial chambers (Fig. 4.11A).

4.4.2 Arrangement and morphology of the filaments [Appendix C, characters 36–37]

Morphologically simple demibranchs consist of identical filaments arranged in a flat, single row connected to the ctenidial axis. However, in numerous bivalves the filaments of a demibranch are thrown into vertical folds or plicae, giving the ctenidia a scalloped appearance. In this case, the portion of each plica that first comes into contact with the inhalant current (i.e. the point that is furthest from the interlamellar space) is referred to as the apex or crest, whereas the depression directed in the opposite direction is considered to mark the limit between adjacent plicae (Ridewood, 1903; Atkins, 1937*c*). In plicate ctenidia, all filaments may display the same morphology or, more commonly, those occupying depressions and apexes are larger and differentiated from the remaining, ordinary filaments (Fig. 4.11C–F). Differentiated filaments in a depression and apex are termed principal and apical filaments, respectively.

Anomalodesmatan ctenidia are, in the great majority, plicate with principal filaments, and in many cases apical filaments are also present. Flat ctenidia appears to be common only in septibranchs (see Allen & Turner, 1974; Morton, 2003*b*). Among taxa investigated herein, flat ctenidia were found only in the thraciid *Parvithracia suteri*, whereas in *P. fragilissima* the outer demibranch is flat and the inner plicated.

4.4.3 Ctenidial unions [Appendix C, characters 39–42]

Unions among ctenidial filaments and between the borders of the gills and the body wall are very common across the Bivalvia and, similar to union of the pallial epithelium, they may be ciliary, cuticular, or tecidual.

In all heterodonts, including anomalodesmatans, unions among filaments are invariably tecidual. These epithelial fusions occur at regular distances among filaments of a lamella (interfilamentar junctions), giving the gills a reticulate appearance, and they may additionally link abfrontal surfaces of filaments in distinct lamellae of a demibranch (interlamellar junctions).

Interlamellar junctions in the form of continuous septa (Fig. 4.11B, D), extending dorsally from the ventral margin of the inner demibranch, occur in most anomalodesmatans with filamentous ctenidia but are apparently absent in several verticordiids (Ridewood, 1903; Allen & Turner, 1974).

While all junctions among filaments are tecidual in anomalodesmatans, those involving the margins of the gills are more commonly ciliary or cuticular (Morton, 1985*a*). Connections of the margins of the gills occur both between demibranchs and the body wall, and between left and right inner demibranchs (or left and right internal borders of the septum) posterior to the foot. The type of union along these areas may be dif-

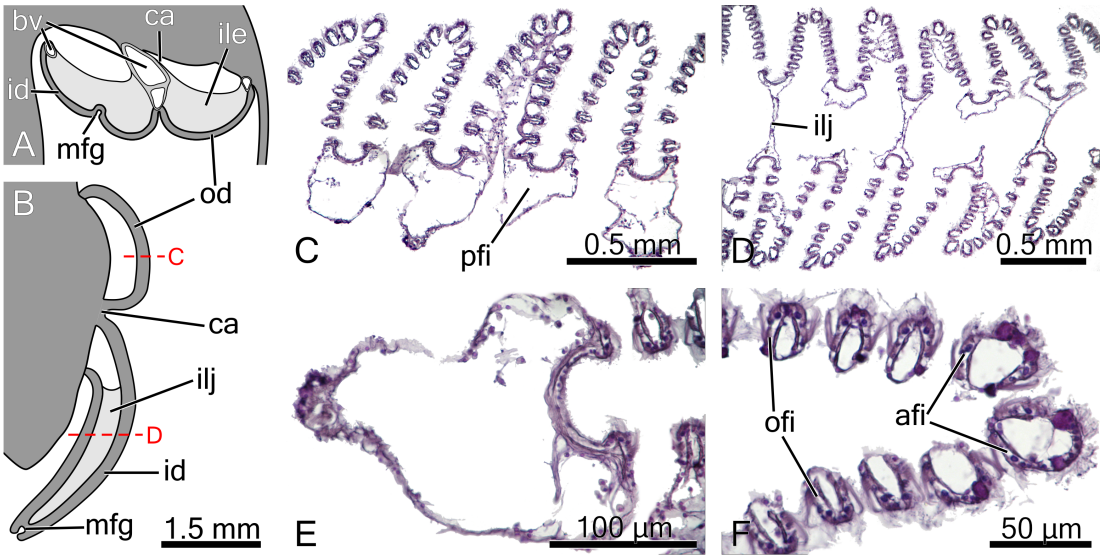


Figure 4.11: **A**. Diagrammatic transverse section through the ctenidium and adjacent body wall of *Euciroa eburnea*, showing the horizontal alignment of the filaments. Redrawn after Ridewood (1903, fig. 55a). **B**–**F**. *Lyonsia norwegica*, BMNH 20070070. **B**. Diagrammatic transverse section through the ctenidium and adjacent body wall, showing the vertical alignment of the filaments. **C**–**D**. Histological sections through the outer and inner demibranchs, respectively, analogous to those indicated by the respective dashed lines in **B**. **E**–**F**. Detail of principal and apical filaments, respectively. Abbreviations: **afi**, apical filament; **bv**, blood vessel; **ca**, ctenidial axis; **id**, inner demibranch; **ile**, interlamellar extension of filament; **ilj**, interlamellar junction; **mfg**, marginal food groove; **od**, outer demibranch; **ofi**, ordinary filament; **pfi**, principal filament.

ferent. In *Laternula elliptica*, for example, cuticular union characterises the junctions of both demibranchs to the body wall, but posterior to the foot left and right inner demibranchs are fused by tissue.

At the posterior end of the ctenidia, the outer demibranchs connect laterally to the membranous pallial extension that divides the proximal apertures of the inhalant and exhalant siphons (intersiphonal septum). However, the posterior tips of the ctenidial axes and inner demibranchs seem to hang free in all anomalodesmatans bearing ctenidia, so that a permanent division between infra and supra-branchial chamber does not exist between inner demibranchs and intersiphonal septum. Sartori & Domaneschi (2005) termed this communication inter-chamber aperture. It was found herein that in a few anomalodesmatans (*Thraciopsis angustata*, *Hunkydora novozelandica*, *Myadora brevis* and *Periploma compressum*) a tentacular projection develops on each side of the septum which partially divides the sector united to the outer demibranchs from the inter-chamber aperture (Fig. 4.12A).

4.4.4 Morphology of the labial palps [Appendix C, characters 44–46]

Labial palps are appendages of the mouth which in almost all bivalves sort food particles brought into the pallial cavity. Primitively there is a pair of palps on each side of the mouth and these are normally broad and flattened, approximately triangular, and with sorting ridges and grooves on their oralward faces (Fig. 4.6).

In carnivorous anomalodesmatans, however, the labial palps may be greatly modified. In *Cardiomya cleryana*, for example, only one palp is recognisable on each side of the mouth, and this is completely devoid of ridges and tentacular in shape rather than leafy (Fig. 4.10). In other carnivorous taxa, palps may retain a triangular shape but be devoid of sorting areas (Morton, 2003*b*), or they may be reduced but display a few ridges on their oralward face (Morton, 1982).

Being projections of the buccal lips, labial palps are generally positioned adjacent to the mouth. This is true of all anomalodesmatans excepting pandorids, whose palps are separated from the mouth by long proximal oral grooves (Allen, 1954; Morton, 1984*d*).

4.4.5 Marginal food groove and association of gills to labial palps [Appendix C, characters 38, 43]

In filter-feeding bivalves, the gills are responsible not only for generating a water current through the pallial cavity, but also for capturing, sorting and transporting particles to the labial palps and mouth. These processes are accomplished by ciliary mechanisms, and oralward transport of particles may occur along a morphologically undifferentiated surface, or it may take place in marginal grooves positioned in between lamellae.

Anomalodesmatan ctenidia typically bear a deep food groove along the margin of the inner demibranch (Fig. 4.11A, B), but this structure is lacking in some carnivorous taxa (e.g. in *Bentholyonsia teramachii* Morton, 2003*b*).

Delivery of particles to the labial palps is facilitated by the close contact between these organs and the gills. In a comparative study of this relationship, Stasek (1963*b*) noted three distinct categories of association of the ventral tips of the anterior filaments of the inner demibranchs and the distal oral grooves in between outer and inner labial palps. His types I and II are characterised by the ventral tips of the filaments inserted unfused and fused into the groove, respectively, and his type III is defined by ventral tips not inserted into the distal oral groove, although the antero-ventral margin of the inner demibranch may be fused to the inner palp lamella.

With the exception of a few species of *Lyonsia*, which display a relationship of type II between palps and gills (*L. norwegica* examined herein; *L. californica* described by Narchi, 1968), all anomalodesmatans typify Stasek's (1963*b*) category III (Fig. 4.6).

4.5 Foot and statocysts

4.5.1 Byssal apparatus in adults [Appendix C, character 47]

The ability to produce byssal threads is an early post-larval feature whose paedomorphic retention into adulthood played a paramount role in the radiation of bivalves into epifaunal life styles (Yonge, 1962; Stanley, 1972).

In anomalodesmatans, adult byssal attachment is known only in some lyonsiids and septibranchs (Yonge, 1952; Ansell, 1967; Allen & Turner, 1974; Leal, 2008), but a conspicuous byssal groove running along the sole of foot (Fig. 4.10) and associated gland at the heel of the organ (Fig. 4.12C) are also present in pholadomyoids (Morton, 1980, 1982) and pandorids (Allen, 1954; Boss & Merrill, 1965; Morton, 1984*d*). Conversely, in thraciids, myochamids, cleidothaerids, clavagelloids and periplomatids only a tiny pore might be present at the heel of the foot but no associated gland is visible in histological sections (Fig. 4.12B).

4.5.2 Opisthopodium [Appendix C, character 48]

The opisthopodium is an unpaired appendage that projects from the border of the visceral mass, posterior to the foot (Fig. 4.6). The organ was previously described in *Pholadomya candida*, *Halicardia flexuosa*, *H. nipponesis*, *Periploma ovatum* and *Poromya eximia* (Dall, 1895; Pelseneer, 1911; Nakazima, 1967; Morton, 1980) and, as far as I know, has never been found outside Anomalodesmata. Morton (1980) noted nerve cords running along the opisthopodium of *P. candida* and suggested the appendage is probably a sense organ that monitors the inhalant current.

The present investigation revealed that the thraciid *Asthenothaerus maxwelli* and the periplomatid *P. compressum* also bear opisthopodia, but I failed to find nerves in histological sections of the organ in these taxa.

4.5.3 Pedal retractors [Appendix C, character 49]

The foot of extant heterodonts is withdrawn into the pallial cavity by anterior and posterior pairs of retractor muscles, which typically attach to the internal surface of the shell dorsal to the adductor musculature (Fig. 4.13).

This condition characterises most, but not all anomalodesmatans. Hence, in pandorids the insertion areas of both pairs of pedal retractors are located ventral to the adductors (Allen, 1954; Boss & Merrill, 1965; Morton, 1984*d*). In *Bentholyonsia teramachii*, the posterior pedal retractor retain its plesiomorphic topology, but the anterior retractor attaches to the shell posterior to the anterior adductor (Morton, 2003*b*).

In the present investigation, a unique position of insertion of the posterior pair of pedal retractors was found in *Hunkydora novozelandica* and *Myadora brevis*. Both

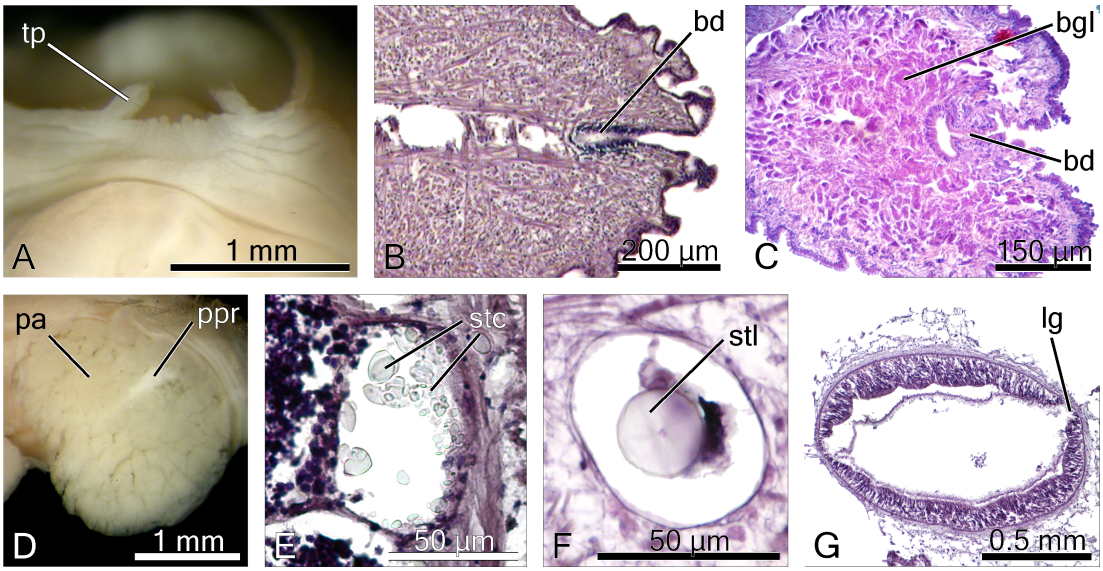


Figure 4.12: **A**, **B** and **D**. *Hunkydora novozelandica*, NMNZ M. 183056. 2004030. **A**. Anterior border of the intersiphonal septum, showing a pair of tentacular projections which partially delimit the inter-chamber aperture. Ctenidia removed. **B**–**C**. Transverse sections through the heel of the foot of *H. novozelandica* and *Lyonsia norwegica* (BMNH 20070070), respectivel, showing a vestigial byssal duct in the former and a large byssal gland in the latter species. Dorsum towards the left in both subfigures. **D**. Left view, showing the proximal end of the posterior pedal retractor emerging in the middle of the posterior adductor muscle. **E**–**F**. Sections through one of the statocysts of *Thraciopsis angustata* and *Cardiomya cleryana* (CENEMAR, unregistered; Santos, SP, to São Francisco do Sul, SC, Brazil), respectively, showing numerous statoconia in the former and a single statolith in the latter species. **G**. *Lyonsia norwegica*, BMNH 20070070. Transverse section through the oesophagus, showing lateral grooves of the internal epithelium. Abbreviations: **bd**, byssal duct; **bgl**, byssal gland; **lg**, lateral groove; **pa**, posterior adductor; **ppr**, posterior pedal retractor; **stc**, statoconia; **stl**, statolith; **tp**, tentacular projection.

myochamids have these muscles attached to the shell among fibres of the posterior adductor (Fig. 4.12D).

4.5.4 Statocysts [Appendix C, character 50]

The structure of anomalodesmatan statocysts has been studied comparatively by Morton (1985*b*), who recognised five different categories based on the histology of the organs.

Among these, type A is by far the most complex, comprising a cellular statolith with epithelial invaginations that form two secretory tubules. It is exclusive of *Pholadomya candida* and its description based on a single specimen whose fixation was not appropriate for fine histological work (see Morton, 1980). Hence, although some anatomical features of *P. candida* are remarkable and unique among bivalves (e.g. the arrangement of its pallial musculature around the pedal opening; see Morton, 1980),

the possibility cannot be excluded that the unusual features of this type of statocyst are due to methodological artefacts.

The remaining statocyst morphologies were divided by Morton (1985*b*) into types B and C based on the histology of the capsule, and B split into three sub-types (B_1, B_2 and B_3) on the basis of statolith structure.

Type C is exclusive to cuspidariids and defined by a capsule comprising only 4 or 5 swollen cells, fringed by a narrow (1–2 μm) border of microvilli, and containing a single basophilic statolith (Morton, 1985*b*).

Type B comprises a multicellular capsule of ciliated cells with either a single basophilic statolith (B_1), multiple basophilic statoconia (B_2), or multiple statoconia that do not take up stains and appear inorganic (B_3).

In my comparative survey, fixation of material was rarely good enough to allow confident assessment of the number of cells forming statocyst capsules or whether they are lined by cilia or microvilli. Attempts to distinguish types B and C were thus abandoned.

In every taxon examined herein, including the cuspidariid *Cardiomya cleryana*, statolith and statoconia appeared inorganic, did not take up stains (Fig. 4.12E, F) and their behaviour under cross-polarised light suggested that they are anisotropic. The similar aspect and shape of these elements suggest that they are all secreted by the animal, probably as calcium carbonate crystals in an organic matrix, as in other molluscs (Wiederhold *et al.*, 1990; Bettencourt & Guerra, 2000; Zacherl *et al.*, 2003). It is thus at least plausible that the difference between basophilic and inorganic statoconia is artefactual because, had the specimens analysed herein been decalcified (as is common in material preserved and processed for histology) the organic matrix of statoconia would be free to take up stains and appear basophilic.

Hence, in comparing anomalodesmatan statocysts I have only taken into account the number of elements in each capsule and found several statoconia in all examined taxa but *Cardiomya cleryana*, which displayed only one large, spherical statolith in each statocyst (Fig. 4.12F).

4.6 Digestive tract

4.6.1 Oesophagus [Appendix C, character 51]

Two different oesophageal morphologies were found during the present comparative survey. The first comprises a flattened tube with longitudinal ridges running along the dorsal and ventral walls of the lumen, and separated by left and right grooves of the internal epithelium (Fig. 4.12G). This configuration was recorded in all examined

taxa but the cuspidariid *Cardiomya cleryana* and the parilimyid *Parilimya neozelanica*, both of which displayed a cylindrical oesophagus with smooth internal epithelium.

Illustrations of histological sections through the oesophagus of *Pholadomya candida* by Morton (1980) suggests the species bears an oesophagus of the second type.

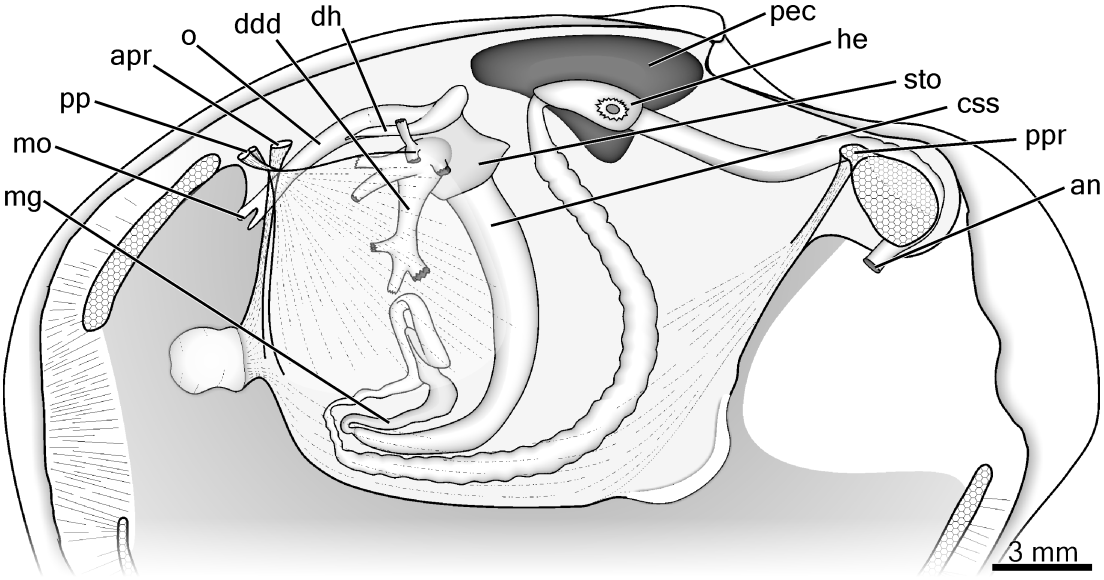


Figure 4.13: *Periploma compressum*, CENEMAR, unregistered (Bombinhas, Brazil). Left view of a dissected specimen, showing the pedal musculature and the path and components of the digestive tract. Abbreviations: **an**, anus; **apr**, anterior pedal retractor; **css**, crystalline style sac; **ddd**, digestive diverticula duct; **dh**, dorsal hood; **he**, heart; **mg**, midgut; **mo**, mouth; **o**, oesophagus; **pec**, pericardial cavity; **pp**, pedal protractor; **ppr**, posterior pedal retractor; **sto**, stomach.

4.6.2 Stomach [Appendix C, characters 52–54]

The bivalve stomach is a complex organ, divided into two portions of distinct morphology and function. The first portion, referred to as stomach vestibule or simply the stomach (Fig. 4.13), connects to both oesophagus and digestive diverticula, a system of branching, blind-ending tubules where absorption and intracellular digestion takes place (Owen, 1955). The stomach vestibule is saccular in form and its internal epithelium normally bear a number of sorting ridges and grooves, which direct accepted particles to the digestive diverticula ducts and rejected particles to the intestine. Additionally, the left wall of the organ is generally lined by a protective covering, the gastric shield, against which a gelatinous rod, the crystalline style, acts (Purchon, 1956).

The second portion of the stomach, termed style sac, is a cylindrical extension of the ventral wall of the vestibule which produces and moves the crystaline style. Rotation of the style against the gastric shield macerates food particles and dissolves the style,

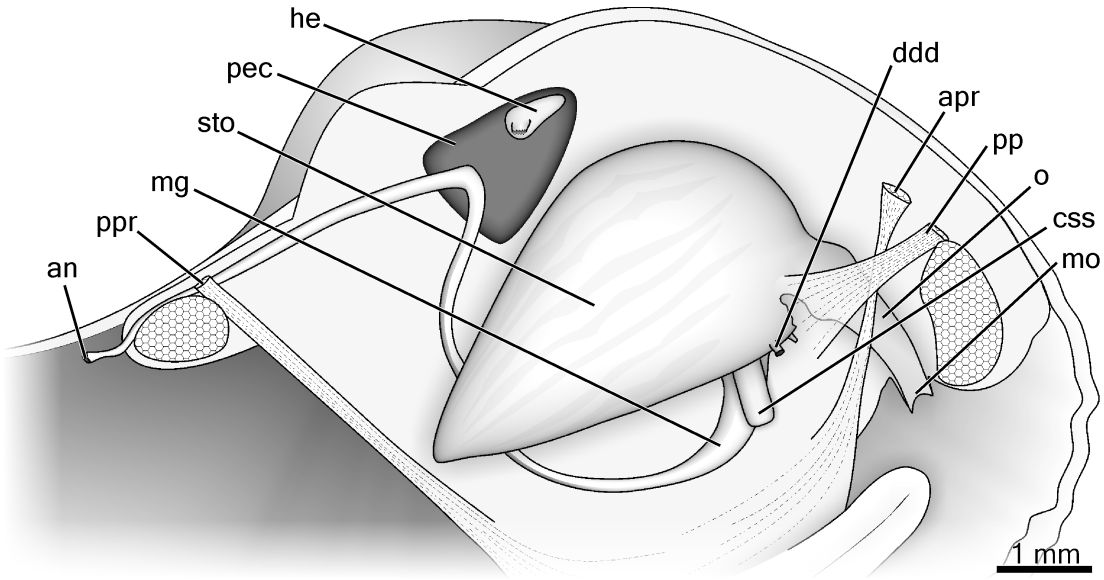


Figure 4.14: *Cardiomya cleryana*, CENEMAR, unregistered (Santos, SP, to São Francisco do Sul, SC, Brazil). Right view of a dissected specimen, showing the pedal musculature and the path and components of the digestive tract. Abbreviations: **an**, anus; **apr**, anterior pedal retractor; **css**, crystalline style sac; **ddd**, digestive diverticula duct; **he**, heart; **mg**, midgut; **mo**, mouth; **o**, oesophagus; **pec**, pericardial cavity; **pp**, pedal protractor; **ppr**, posterior pedal retractor; **sto**, stomach.

releasing extra-cellular enzymes bound up in its matrix (Morton, 1973*b*). The style sac may be either completely separated from the intestine, or its lumen may be partially separated from that of the midgut by epithelial typhlosoles (minor on the right and major on the left sides). In some taxa, one or both of these typhlosoles may extend into the stomach and digestive diverticula.

The bivalve stomach has been the focus of several comparative studies (e.g. Graham, 1949; Reid, 1965; Dinamani, 1967; Purchon, 1956, 1957, 1958, 1960*b*, 1987), which revealed numerous variations in the features summarised above. Purchon (1956, 1957, 1958, 1960*b*, 1987) systematically surveyed stomach morphology across the class and recognised five basic types, two of which are displayed by anomalodesmatans.

Stomach type IV, regarded as plesiomorphic for Heterodonta (Purchon, 1987), is characteristic of filter-feeding anomalodesmatans. It is chiefly defined by a major typhlosole "which emerge from the mid gut and curve evenly to the left across the stomach floor, without production of a typhlosolar tongue and without entering into an embayment on the right anterior side of the stomach" (Purchon, 1987, p. 184).

Stomach type II was originally described in cuspidariids and poromyids, and defined by numerous features, including (1) a small style sac, (2) a compact crystalline style which does not project far into the stomach, (3) lack of a dorsal hood (a dorsal em-

bayment of the wall of the stomach), (4) lack of a gastric shield, (5) two slender ducts from the digestive diverticula opening on the anterior floor of the stomach, (6) lack of conspicuous sorting areas and (7) only one typhlosole which does not extend into the stomach (Purchon, 1956). However, with subsequent studies of additional septibranch taxa, it became clear that several may display plesiomorphic features found in other stomach types. Hence, regarding the stomach of verticordiid genera assigned to type II, Purchon (1987, p. 185) remarks "individual species show different degrees of specialization towards the carnivorous habit, those least specialized having stomachs that still possess a dorsal hood, a small sorting area of ciliated folds, a small major typhlosole and an intestinal groove".

But the most serious difficulty encountered in this division of anomalodesmatan stomachs into two types has been the stomach architecture of the arguably carnivorous parilimyid *Parilimya fragilis*, described by Morton (1982). The stomach of the species has an anterior portion that is very similar to that of a type IV stomach, with a major typhlosole projecting well into the anterior floor of the stomach and curving to the left, and the presence of a conspicuous crystalline style and sac, dorsal hood, gastric shield and left pouch (an embayment on the left wall of the stomach). And yet, the posterior portion of the organ is modified into a muscular sac with longitudinal folds, being very similar in that respect to a stomach of type II. Purchon (1987, p. 226) discussed the possibilities of regarding the stomach of the species as type IV or II and concluded "neither of these is satisfactory".

Hence, instead of following a somewhat artificial dichotomy between types IV and II as did Morton (1985*a*) and Harper *et al.* (2000), I attempted to recognise discrete variation in morphological features encompassed in the definition of these types and defined three characters of interest: (1) presence of musculature on the posterior wall of the stomach; (2) whether the style sac and midgut are conjoined; and (3) an isolated duct from the digestive diverticula opening on the left floor of the stomach.

Among taxa analysed herein, the posterior wall of the stomach is expanded into a muscular sac only in the cuspidariid *Cardiomya cleryana* and parilimyid *Parilimya neozelanica* (Fig. 4.14). This trait also characterises all septibranchs (Allen & Turner, 1974; Allen & Morgan, 1981).

The openings of the style sac and midgut on the floor of the stomach are conjoined in all anomalodesmatans. However, in most taxa the two organs remain united to the distal end of the style sac, whereas in some cuspidariids and poromyids, they split immediately after leaving the ventral wall of the stomach (Yonge, 1928).

Ducts from the digestive diverticula typically connect to the stomach at embayments of the left and right walls (caeca). In the thraciid *Asthenothaerus maxwelli* and myochamid *Hunkydora novozelandica*, as well as in cleidothaerids, periplomatids,

thraciids and pandorids described in the literature (Allen, 1954, 1958; Morton, 1973*a*; Sartori & Domaneschi, 2005), an isolated duct is present on the left side of the stomach floor, which is approached by the major typhlosole.

4.6.3 Path of the intestine [Appendix C, characters 55–56]

In most bivalves the intestine passes through the ventricle of the heart as it travels posteriorly to end near the proximal end of the exhalant aperture (Fig. 4.13). However, in a few anomalodesmatans, including *Pholadomya candida*, *Cardiomya cleryana* and *Bentholyonsia teramachii*, the intestine passes below the ventricle (Morton, 1980, 2003*a*), whereas in *Cleidothaerus maorianus* and pandorids it passes above the heart (Morton, 1974; Boss & Merrill, 1965).

The path of the intestine between the midgut and the pericardial cavity is also variable. In leaving the ventral wall of the stomach, the midgut passes ventrally into the visceral mass and may either curve posteriorly and ascend to the pericardial cavity (Fig. 4.14), or it may travel anteriorly and perform a few loops before continuing towards the heart (Fig. 4.13). Amongst taxa surveyed here, the former path was only recorded in the lyonsiid *Lyonsia floridana* and in *Cardiomya cleryana*.

4.7 Reproduction [Appendix C, characters 58–59]

Hermaphroditism with separate male and female gonads and ducts was early recognised as the typical configuration of the reproductive system of anomalodesmatans (Pelseneer, 1891*b*, 1895).

Apart from cuspidariids, which are all dioecious (Bernard, 1974), only the clavagellid *Clavagella australis* and the lyonsiellid *Bentholyonsia teramachii* have been described as having separate sexes, both on the basis of histological examination of single specimens (Morton, 1984*a*, 2003*b*).

Across Anomalodesmata, male and female gonadial apertures have been variably described as either separated from one another and from the discharge opening of the kidneys, united to one another but separated from the nephridiopore, or joined in a urogenital papilla. Harper *et al.* (2000) considered this variation phylogenetically informative and coded a character using the three conditions listed above as states.

However, regardless of the configuration of the apertures, anomalodesmatan gonadial and nephridial ducts are invariably separated. Taxa with separate apertures have these openings positioned very close to one another (e.g. Sartori & Domaneschi, 2005, fig. 14). Thus, it seems to me that variations in the degree of union among urogenital apertures may reflect distinct interpretations of material affected by contraction upon preservation rather than heritable differences in the configuration of the apertures.

In most anomalodesmatans large oocytes are individually surrounded by a thick, gelatinous layer or capsule, which forms during vitellogenesis and is thought to correspond to a vitelline membrane (Bigatti *et al.*, 2001; Sartori & Domaneschi, 2005). Larval development takes place, at least initially, within this capsule, which is demersal in the few anomalodesmatans whose larvae have been studied (Allen, 1961*b*; Ansell & Harvey, 1997; Chanley & Castagna, 1966; Gustafson *et al.*, 1986; Peck *et al.*, 2007).

Although numerous suggestions have been made that anomalodesmatans might brood their offspring in their spacious supra-branchial chamber (e.g. Burne, 1920; Morton, 1982), developing embryos have never been found in the pallial cavity of preserved specimens and spawning has been observed in all species for which aspects of their reproductive biology are known.

Chapter 5

Cladistic analysis

Despite recent efforts, the phylogenetic relationships of anomalodesmatans remain enigmatic (see chapter 1 for a historical review of the systematics of the group).

Harper *et al.* (2000) published the first cladistic study of extant representatives of the group based on analyses of an explicit dataset, including 43 conchological and anatomical characters distilled from the literature. Their results corroborated the monophyly of all five major component taxa listed in most classifications (Pholadomyoidea, Thracioidea, Pandoroidea, Clavagelloidea and Septibranchia), but did not support established views of their interrelationships. However, subsequent molecular surveys by Dreyer *et al.* (2003) and Harper *et al.* (2006) produced very different cladograms for the group, in which only Clavagelloidea was supported as monophyletic. Other recovered groups differed from all previously advocated hypotheses of anomalodesmatan relationships and morphological synapomorphies for the new clades could not be recognised (Dreyer *et al.*, 2003; Harper *et al.*, 2006). Notwithstanding such surprising results and lack of support in previous systematic treatments, these authors have argued that (1) "Palaeontological and molecular data are compatible whereas homology decisions for morphological characters need re-evaluation" (Dreyer *et al.*, 2003, p. 244); and (2) "There is definite need to improve our knowledge of the distribution of morphological characters" (Harper *et al.*, 2006, p. 416).

The previous analytical chapters in this volume documented the results of an exhaustive survey of all major organ systems within Anomalodesmata, reassessing hypotheses of primary homology and expanding taxonomic sampling considerably. In this chapter the resulting enhanced matrix of redefined morphological characters is subjected to cladistic analyses with the aim of testing whether the conflicting results attained in previous studies are due to insufficient taxonomic sampling and inappropriate character analysis of morphological data. Additionally, if at least some of the clades suggested by the molecular studies are recovered herein, the present analysis

should indicate their synapomorphies, which is fundamental if we are to place new, unsequenced and, ultimately, fossil anomalodesmatans into a natural classification.

5.1 Material and methods

5.1.1 Taxonomic sampling

The present analyses include representatives of all extant families currently purported to belong in Anomalodesmata, totalling 40 species. Due to the low abundance of most anomalodesmatans and relative paucity of published morphological data on members of the group, choice of representative taxa within each family was dictated by the availability of specimens and/or published anatomical accounts.

With the exception of Cuspidariidae, all families are represented by at least one terminal of the type genus and, in some cases, the type species has been included (see Table 5.1).

Three outgroups — Palaeoheterodonta, Archiheterodonta and Tellinoidea — were chosen based on previously advanced phylogenetic hypotheses for bivalve higher groups, discussed in section 1.2.1 and summarised by Figure 1.6. Tellinoidea was chosen as a representative taxon within the Veneroida + Myoida sister-group of Anomalodesmata because numerous individuals of *Tellina fabula* were available for dissection.

Sources of data for each included taxon are listed in Table 5.1. Original observations were based on museum specimens and material presented by colleagues or collected by the author. Collection data for these specimens is presented in Appendix A. Material currently in possession of the author will be deposited in museum collections before publication of this study in a scientific journal.

Table 5.1: Sources of morphological data for each terminal taxon scored in the present study. Three outgroup taxa (Palaeoheterodonta, Archiheterodonta and Tellinoidea) were coded using a groundplan approach. For these terminals, the actual species from which data was obtained are listed in the right column (data sources). For taxa scored from original observations, collection data of the examined specimens is given in Appendix A. Type species of families are indicated by * and of genera by °.

Coded terminal	Data sources
Palaeoheterodonta	*Anodonta anatina* — Original observations: most characters *Margaritifera margaritifera* — Le Pennec & Jüngbluth (1983): ligament *Neotrigonia margaritacea* — Morton (1987*c*): gill connections *Unio* sp. — Bhamrah & Juneja (2003): statocyst various species — Graf & Cummings (2006): hinge teeth; brooding
Archiheterodonta	*Cardita ventricosa* — Yonge (1969): most characters *Crassinella mactracea* — Allen (1968): pallial pigmentation *Astarte sulcata* — Atkins (1937*b*): gill connections; Purchon (1958): stomach

Coded taxon	Data sources
	Cardita variegata — Pelseneer (1911): statocyst various species — Taylor *et al.* (1973): shell microstructure
Tellinoidea	*Tellina fabula* — Original observations: most characters *Tellina petitiana* — Barón & Ciocco (1997): histology of siphons *Asaphis deflorata* — Domaneschi & Shea (2004): gill connections *Macoma baltica* — Lammens (1968): statocyst various species — Trueman (1966): ligament; Taylor *et al.* (1973): shell microstructure; Ridewood (1903): histology of gills
	PHOLADOMYOIDEA
	Pholadomyidae
*Pholadomya candida**	Original observations: conchological and pallial characters Morton (1980): remaining characters
	Parilimyidae
Parilimya fragilis	Morton (1982)
Parilimya neozelanica	Original observations
Parilimya sp1	Krylova (2006)
	THRACIOIDEA
	Thraciidae
Thracia meridionalis	Original observations: conchological characters Sartori & Domaneschi (2005): remaining characters
Asthenothaerus maxwelli	Original observations
Parvithracia fragilissima	Original observations
Parvithracia suteri°	Original observations
Thraciopsis angustata°	Original observations
Trigonothracia jinxingae	Original observations: conchological and histological characters Morton (1995): remaining characters
	Periplomatidae
Periploma compressum	Original observations
Cochlodesma praetenue	Allen (1958)
Offadesma angasi°	Morton (1981*a*)
Pendaloma micans°	Original observations: anatomical characters Marshall (2002): conchological characters
	Laternulidae
Laternula elliptica	Original observations; Sartori, Passos & Domaneschi, unpublished
Laternula truncata	Original observations: conchological, pallial and gross anatomical characters Morton (1973*a*): remaining characters
	PANDOROIDEA
	Pandoridae
*Pandora inaequivalvis**	Allen (1954)
Pandora filosa	Thomas (1994)
Pandora gouldiana	Boss & Merrill (1965)

Coded taxon	Data sources
Frenamya ceylanica	Morton (1984*d*)
	Lyonsiidae
Lyonsia floridana	Original observations
*Lyonsia norwegica**	Original observations
	Cleidothaeridae
Cleidothaerus maorianus	Morton (1974)
*Cleidothaerus albidus**	Morton & Harper (2001): shell microstructure and mantle Hancock (1853*a*): gross anatomy
	Myochamidae
Hunkydora novozelandica°	Original observations
Myadora brevis°	Original observations: most characters; Taylor *et al.* (1973): shell microstructure
*Myochama anomioides**	Harper & Morton (2000): most characters Hancock (1853*b*): gross anatomy
	Clavagelloidea
	Clavagellidae
Brechites vaginiferus	Original observations: conchological characters Morton (1984*b*, 2002*a*): remaining characters
Clavagella australis°	Morton (1984*a*)
Dianadema multangularis°	Original observations: conchological characters Morton (2003*a*)
Humphreyia strangei°	Original observations: conchological characters Morton (1984*b*, 2002*b*): remaining characters
	Septibranchia
	Verticordiidae
Verticordia triangularis	Allen & Turner (1974)
Bentholyonsia teramachii°	Morton (2003*b*)
Lyonsiella formosa	Allen & Turner (1974) Morton (1984*c*)
Euciroa pacifica	Dall (1895)
	Cuspidariidae
Cardiomya cleryana	Original observations
	Poromyidae
*Poromya granulata**	Original observations: conchological characters Allen & Morgan (1981): remaining characters
	Uncertain superfamily
	Spheniopsidae
Grippina californica°	Original observations
Spheniopsis frankbernardi	Original observations
	Uncertain family
Thracidora arenosa°	Original observations

5.1.2 Character analysis and coding

Character formulation was based on original observations, combined with an exhaustive survey of literature concerning anomalodesmatan morphology and systematics. Characters were also distilled from a more general inspection of literature on bivalve morphology in general, particularly cladistic analyses (e.g. Schneider, 1995; von Salvini-Plawen & Steiner, 1996; Schneider, 1998*a*,*b*; Waller, 1998; Giribet & Wheeler, 2002; Tëmkin, 2006; Mikkelsen *et al.*, 2006) and comparative studies of organ systems.

Only characters showing well-defined, discrete variation among terminal taxa were kept in the present analyses. Although at least one currently available computer program for parsimony inference is able to cope with continuous characters (TNT, see Goloboff *et al.*, 2006), confidence intervals are required to avoid counting steps for changes of mean values whose difference is not statistically significant (Farris, 1990). Severe limitations in the number of specimens available for examination and the qualitative nature of most literature accounts of anomalodesmatan anatomy precluded the calculation of meaningful confidence intervals for observed continuous features. Hence, these characters were not used in the analyses but some will be discussed in the light of the resulting cladograms.

Similarly, in cases where changes in a character are required for the formation of another, or leads to a compensatory change in another character, the features were considered dependent and the least informative in each pairwise comparison (the character with more missing data, less states or least complex morphology) excluded from analysis.

Character complexes commonly used in morphological studies of bivalves, such as gills, stomach and statocyst types, were dissected into constituting characters and scored independently.

In total, 59 parsimony informative characters were selected. Definition of these characters and their states are presented in Appendix C and a discussion of each can be found in the previous chapters of this volume.

All ingroup taxa were coded using species as terminals as this approach does not assume monophyly of supraspecific groups, is easily repeatable and facilitates integration of the present matrix with molecular datasets in future studies of the group. For the operational outgroups, a groundplan approach to character coding was used to minimise the amount of missing data in the dataset, since testing the monophyly of these outgroup taxa was not one of the objectives of the present analysis (see Prendini, 2001, for a review of these two approaches).

In a few occasions, discrepancies were found among published morphological studies of the same species or between previously reported and original observations. In these

Table 5.2: Data matrix. Dashes (-) and question marks (?) indicate inapplicable and missing data, respectively. See Appendix C for definitions of characters and states.

	5	10	15	20	25	30	35	40	45	50	55	
Palaeoheterodonta	00-00	--010	00110	110-0	0001-	10000	--000	00100	?1001	10000	10000	0010
Archiheterodonta	00-00	--000	11110	000-0	0001-	00000	--000	00100	0?001	01000	?0001	0?10
Tellinoidea	00-00	--010	11110	00100	00000	00000	10001	00000	21201	00000	10000	0010
Pholadomya candida	00-01	01010	00000	11111	11010	00010	10001	11101	21201	01100	00000	2001
Parilimya neozelanica	00-01	01010	00000	11110	11000	0002?	00001	1010?	?1???	0??0?	0010?	00?1
Parilimya fragilis	00-0?	??0??	00000	??110	11??0	0002?	0?001	1?1?0	?1211	010?0	00100	0001
Parilimya sp1	00-01	?1010	00000	??1??	11??0	0002?	??001	??0??	???10	01?0?	???0?	????
Grippina californica	00-00	--00?	11000	22???	?0???	?????	?????	?????	?????	?????	?????	????
Spheniopsis frankbernardi	00-00	--00?	11000	22???	?0???	?????	?????	?????	?????	?????	?????	????
Thracidora arenosa	00-01	01001	00000	02???	?1???	?????	?????	?????	?????	?????	?????	????
Bentholyonsia teramachii	00-0?	??001	00000	?1100	110?-	0002?	??011	000??	???00	01001	00000	2010
Euciroa pacifica	00-01	??001	00100	?11?0	00??-	1000?	??011	0010?	20?10	0000?	?????	20??
Verticordia triangularis	00-01	?1001	00100	?1100	010?-	10000	??011	0010?	00210	010??	?0100	010?
Lyonsiella formosa	00-01	11001	00000	??100	00000	10120	??011	00102	20210	0100?	?0100	010?
Poromya granulata	00-01	?101?	00100	11100	00010	10100	??11-	---02	2??10	0100?	?0110	010?
Cardiomya cleryana	00-00	--001	01000	22100	00000	10000	0111-	---02	2??10	01000	00110	2111
Brechites vaginiferus	01101	01001	00000	11200	11011	10000	10001	101??	??201	000?1	??00?	000?
Humphreyia strangei	01101	01001	00000	11200	01??1	10000	10001	?????	???01	000?1	1??00	000?
Dacosta australis	0102?	??000	00000	??200	01011	10000	?0001	101?1	??201	00001	??00?	001?
Dianadema multangularis	01001	01000	00000	?1200	01??1	?0000	10001	?????	???01	0?0??	??0??	000?
Laternula elliptica	10-00	--021	00000	11101	01011	11000	10001	11101	21201	01001	10001	0001
Laternula truncata	10-01	21021	00000	11101	01011	11000	10001	111?1	21201	01000	?0001	000?
Lyonsia floridana	00-01	21001	00000	11100	1101-	10000	10001	11101	21201	01001	10000	0001
Lyonsia norwegica	00-01	21001	00000	11100	1101-	10000	10001	11101	21101	01001	10001	0001
Frenamya ceylanica	00-00	--100	00001	??100	000?-	1000?	??001	101??	??201	110?0	???0?	0?01
Pandora inaequivalvis	00-00	--100	00001	11100	000?-	00000	??001	111??	?1201	1102?	?1001	100?
Pandora filosa	00-0?	??101	00001	?11??	0??1-	10000	??001	1?1??	???01	1102?	??001	0?0?
Pandora gouldiana	00-00	--101	00001	111??	00?1-	10000	??001	???0?	???01	1102?	??001	1?01
Periploma compressa	10-01	10021	00000	12101	10100	0000?	01001	1?111	?1201	00101	10001	0001
Pendaloma micans	10-00	--021	00000	?1101	11100	0000?	??001	0001?	??201	0010?	?????	????
Offadesma angasi	10-01	??021	00000	11111	11100	00001	?0001	111?1	?1201	00???	?000?	0001
Cochlodesma praetenue	10-01	1?02?	00000	??10?	001?0	00001	01001	1?1??	???01	0?0?1	?1000	?00?
Trigonothracia jinxingae	00-01	1?021	00000	22100	?01?0	00000	??001	101?1	01201	00001	10000	0000
Thracia meridionalis	00-01	10011	00000	22100	10100	00001	01001	10100	01201	00001	11001	0001
Parvithracia fragilissima	00-01	10001	11000	22100	10100	0000?	01001	10100	01201	00001	10001	0001
Parvithracia suteri	00-01	10001	11000	22100	10100	0000?	??001	0010?	??201	00001	?????	?001
Asthenothaerus maxwelli	00-02	10001	00000	22100	10100	0000?	01001	11101	?1201	00101	11001	0001
Thraciopsis angustata	00-02	10001	11000	12100	10100	0000?	01001	1011?	0?201	00001	10001	0001
Hunkydora novozelandica	00-02	?0001	01000	12100	10100	0000?	01001	10111	?1201	00011	11001	0001
Myadora brevis	00-01	00001	11000	11100	00100	0000?	??001	1011?	?1201	0001?	??00?	000?
Myochama anomioides	00-11	??001	11000	11100	100?0	00000	??001	1?1?0	?1201	0?0?1	?????	0?01
Cleidothaerus maorianus	00-1?	??001	00010	??1??	10010	00000	0?001	1?101	1?201	000??	??001	100?
Cleidothaeus albidus	00-1?	??001	00010	11100	10110	00000	??001	1110?	???01	000??	?100?	??0?

cases, present observations were always preferred, whereas conflicts or ambiguity in literature accounts were coded as missing data. The resultant data matrix is given in Table 5.2

5.1.3 Phylogenetic analyses

Data were analysed using TNT version 1.1 for Windows (Goloboff *et al.*, 2008), assigning equal weight to all characters and treating gaps as missing data. Heuristic searches were performed with 1000 replications of random addition-sequence (RAS) and tree bisection-reconnection (TBR) branch swapping, combined with 50 iterations of the parsimony ratchet and 50 rounds of tree-drifting per replication (see Nixon, 1999; Goloboff, 1999, 2002; Giribet, 2007, for details of these methods). The ratchet was set to re-weight 20% of the characters and 10 trees were held per replication. Two outgroups — Archiheterodonta and Tellinoidea — were operationally analysed as part of the ingroup, and cladograms were rooted at the internode connecting the outgroup taxon Palaeoheterodonta with all remaining terminals.

The consistency index (CI), retention index (RI), strict and majority rule consensus of the resulting cladograms were calculated as usual (e.g. Amorim, 1997). Bremer's (1994) direct measure of branch support, which for each clade is defined as the number of extra steps required to lose that clade in the most parsimonious trees, was calculated using the heuristic procedure outlined above but holding 100 trees up to 10 steps longer than optimal per replication. Values for three clades which were not lost in these suboptimal trees (Anomalodesmata, Pandoridae and Laternulidae) were obtained by constraining these clades to be non-monophyletic and performing new searches of 100 replications each.

Poorly resolved consensus trees are often caused by just one or a few taxa, generally having large proportions of missing data, moving among distant positions in alternative most parsimonious trees (MPTs). Hence, following analyses of the entire dataset, automatic evaluations of alternative prunings of up to 5 taxa (or clades) that increases the number of nodes of the strict consensus tree were performed using TNT algorithm "prunnelsen" (Goloboff *et al.*, 2008). New analyses were subsequently performed excluding taxa identified as "wildcards" by this procedure.

In total, four analyses of the dataset were performed using distinct parameter settings: (1) including all taxa and treating all characters as unordered; (2) including all taxa and treating characters 5 (calcified periostracal sculpture), 18 (ventral mantle fusion) and 29 (hypertrophied siphonal retractors) as ordered; (3) excluding 3 taxa for which only conchological data is available (*Grippina californica*, *Spheniopsis frankbernardi* and *Thracidora arenosa*) and treating all characters as unordered; and (4) excluding 3 taxa for which only conchological data is available and treating characters 5, 18 and 29 as ordered.

5.1.3.1 Character state reconstructions

Reconstructions of character state changes on selected cladograms were performed using WinClada version 1.00.08 (Nixon, 2002). The evolution of characters with more than one most parsimonious reconstruction was studied using both accelerated (ACCTRAN) and delayed (DELTRAN) transformation algorithms. These algorithms represent two opposite extremes among most parsimonious reconstructions, with ACCTRAN and DELTRAN maximizing ambiguous character state changes as close to the root or tips of the cladogram as possible (Agnarsson & Miller, 2008).

Character optimisation in polytomous cladograms (e.g. strict consensus trees) is problematic because alternative dichotomous resolutions of the polytomies may imply different character state changes (Maddison & Maddison, 2005). There is no satisfactory solution for this difficulty, but the problem may be circumvented in a number of ways, which include (1) arbitrarily choosing a dichotomous MPT for optimisation; (2) examining character evolution under every possible resolution of the polytomy, an approach that is only feasible for polytomies involving few clades; (3) randomly resolving polytomies before carrying out optimisation; and (4) treating polytomies as events of multiple speciation, in which case shared similarities among clades involved in the polytomy are accounted for as convergences (Maddison, 1989). The fourth approach was adopted herein.

5.2 Results

The search strategy implemented in TNT yielded trees of minimum length in 883 to 937 out of 1000 replications, completing searches in 6 minutes or less, depending on the assumptions in effect for each analysis. The fact that cladograms of minimum length were found in the vast majority of replications, regardless of the starting tree or taxon addition order, suggests with reasonable confidence that the strategy implemented herein was successful in breaking "islands" of locally optimal trees and sampling the total diversity of the treespace (Goloboff, 1999). It is therefore unlikely that trees shorter than those reported below for each of the separate analyses exist for this dataset.

5.2.1 Scope

The analyses presented in this volume are based on the largest morphological dataset of anomalodesmatan bivalves compiled to date, with 59 informative characters and 37 to 40 species of the clade included in different trials (totalling 1870 cells scored as non-missing data for anomalodesmatan terminals alone). In the only previous investigation of extant anomalodesmatans based on an explicit morphological matrix, 43 characters

and 16 terminals were included, resulting in 663 cells scored as non-missing data (Harper *et al.*, 2000).

In terms of taxonomic sampling the present analyses are also slightly larger than published molecular surveys of the group, which included a maximum of 32 anomalodesmatan species (Dreyer *et al.*, 2003; Harper *et al.*, 2006). More importantly, however, is the fact that every extant family currently purported to belong in the clade is represented in the present dataset by at least one terminal, whereas molecular studies of the group have so far failed to obtain sequences from periplomatids, parilimyids and pholadomyids.

5.2.2 Analyses of the complete dataset

Analysis of the data matrix including all taxa and treating all characters as unordered produced 569 most parsimonious trees (MPTs) of length (L) 182 with a consistency index (CI) of 0.40 and a retention index (RI) of 0.74.

The strict consensus of these trees supports monophyly of Anomalodesmata including Spheniopsidae, and of some of the component superfamilies and families, as indicated in Figure 5.1A. Pandoridae appears in an unorthodox position, basal to the node joining all the remaining extant anomalodesmatans. Lyonsiidae is the only family whose monophyly is rejected under the topology of this cladogram, being paraphyletic relative to Laternulidae.

The same dataset analysed with characters 5, 18 and 29 treated as ordered yielded 823 MPTs (L = 184; CI = 0.39; RI = 0.74), whose consensus is compatible but considerably less resolved than that produced by the previous analysis (Fig. 5.1B).

Majority-rule consensus of MPTs found by ordered or unordered analyses of the complete dataset are also compatible, but differ in the percentages of recovery of each clade (Fig. 5.2). Compared to the strict consensus, the majority-rule consensus produced by analysis of the dataset with all characters treated as unordered resolve relationships in the sister group of Pholadomyoidea further, suggesting (1) a large clade comprising myochamids, thraciids, periplomatids, cleidothaerids and spheniopsids, of which only the last three families are monophyletic; and (2) monophyletic Septibranchia as the sister group of clade 1.

Examination of taxon prunings indicated gain of nodes in the strict consensus tree by exclusion of combinations of *Thracidora arenosa*, Spheniopsidae, Periplomatidae, *Hunkydora novozelandica* and *Thracia meridionalis* for the analysis with all characters treated as unordered, and of *Thracidora arenosa*, Spheniopsidae, Periplomatidae and Pandoridae for the analysis with three ordered characters (Table 5.3).

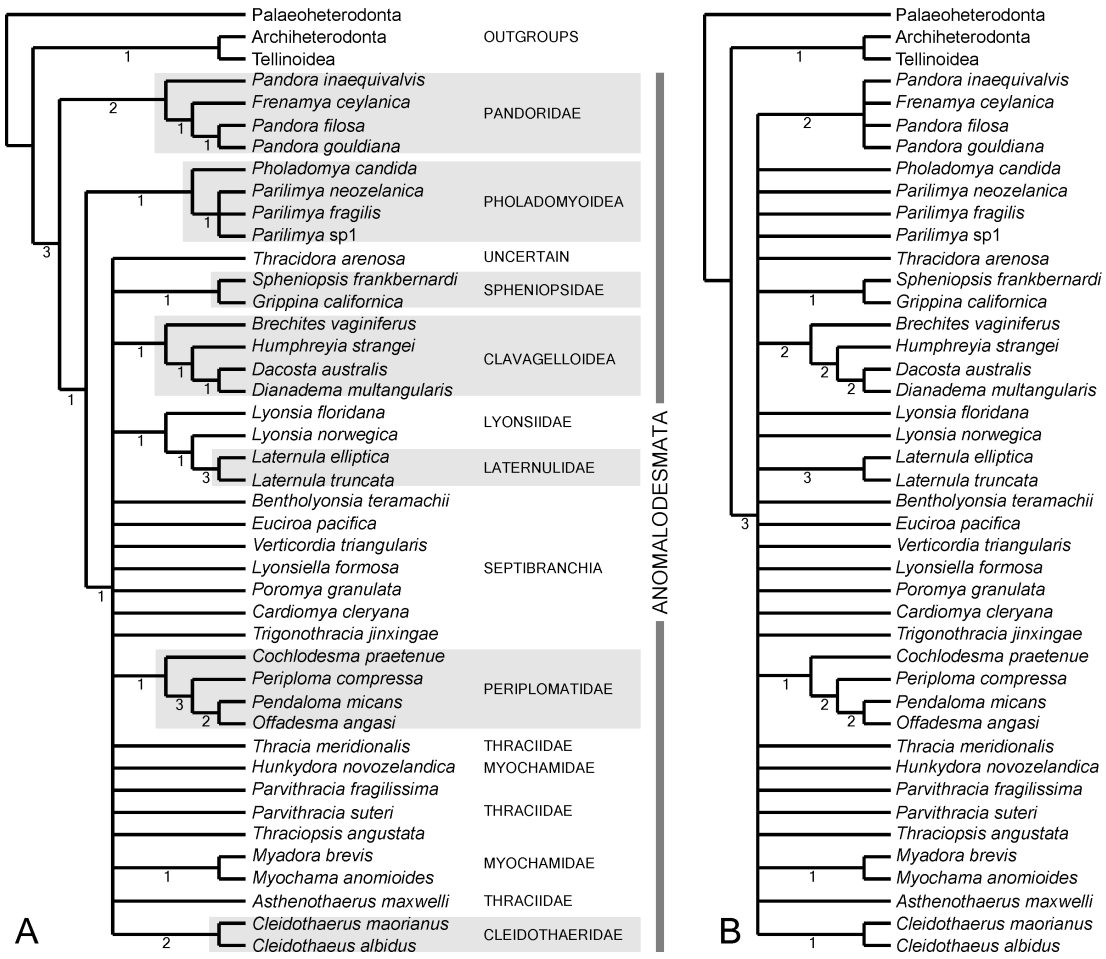


Figure 5.1: Strict consensus of MPTs recovered by analyses of the complete data matrix with all characters treated as unordered (**A**) and with three ordered characters (**B**). Values of Bremer's support index are shown below branches. Traditionally recognised anomalodesmatan superfamilies and families are labelled, and those recovered as monophyletic in **A** indicated by grey rectangles.

With all characters treated as unordered, 2 and 4 nodes are gained by alternative prunings of *Thracidora arenosa* and Spheniopsidae, respectively, whereas simultaneous exclusion of these two clades improves resolution of the strict consensus by 6 nodes. Further improvement in resolution of up to 2 nodes may only be achieved if at least Periplomatidae (comprising four terminals) is pruned from the MPTs.

Pruning of the MPTs produced by analysis of the complete dataset with three characters treated as ordered improves their strict consensus by 4 nodes when Spheniopsidae alone is removed and by 6 nodes when this family is removed simultaneously to Pandoridae (comprising four terminal taxa). The additional exclusions of either *T. arenosa* or Periplomatidae improve resolution of the consensus by one extra step.

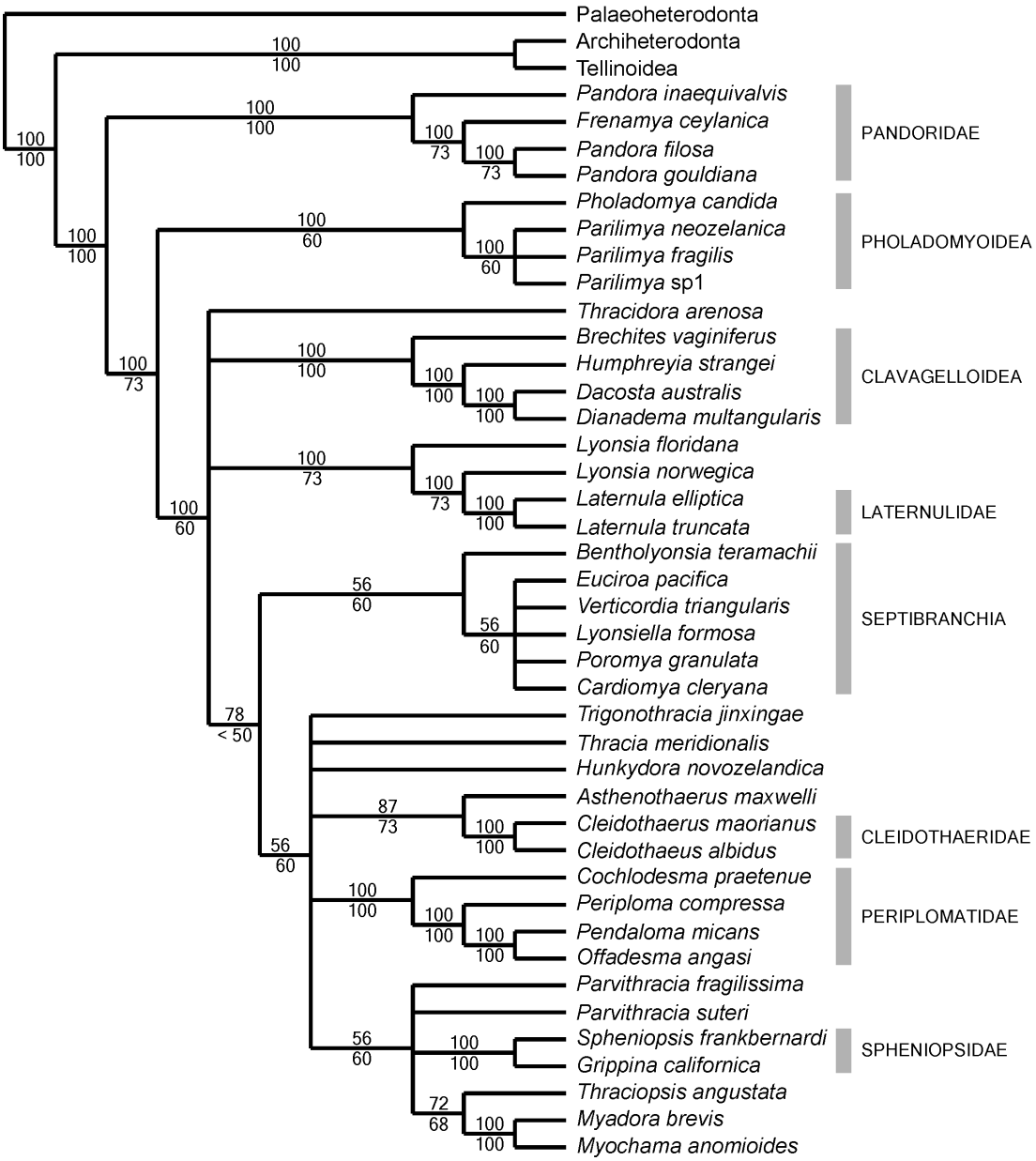


Figure 5.2: Majority-rule consensus of MPTs recovered by analyses of the complete data matrix. Numbers above and below branches denote the percentage of MPTs displaying those branches in analyses with all characters treated as unordered and with three ordered characters, respectively.

Based on these results, *Thracidora arenosa* and the spheniopsid terminals *Grippina californica* and *Spheniopsis frankbernardi*, the three examined taxa with the most missing entries and identified as "wildcards" in both analyses of the complete dataset, were excluded from subsequent analyses.

Table 5.3: List of taxon prunings which resulted in gain of nodes in the strict consensus cladogram produced by analyses of the complete dataset. Column A indicates analyses with unordered characters (U) or with three characters treated as ordered (O). Columns P and N give the total number of prunings and nodes gained, respectively.

A	P	N	Clades pruned
U	1	2	*Thracidora arenosa*
U	1	4	Spheniopsidae
U	2	5	Spheniopsidae, Periplomatidae
U	2	6	*T. arenosa*, Spheniopsidae
U	3	1	*Hunkydora novozelandica*, *Thracia meridionalis*, Periplomatidae
U	3	7	*T. arenosa*, Spheniopsidae, Periplomatidae
U	4	3	*T. arenosa*, *H. novozelandica*, *T. meridionalis*, Periplomatidae
U	4	6	Spheniopsidae, *H. novozelandica*, *T. meridionalis*, Periplomatidae
U	5	8	*T. arenosa*, Spheniopsidae, *H. novozelandica*, *T. meridionalis*, Periplomatidae
O	1	2	Pandoridae
O	1	4	Spheniopsidae
O	2	3	*T. arenosa*, Pandoridae
O	2	5	Spheniopsidae, Periplomatidae
O	2	6	Spheniopsidae, Pandoridae
O	3	7	Spheniopsidae, Pandoridae, Periplomatidae
O	3	7	*T. arenosa*, Spheniopsidae, Pandoridae
O	4	8	*T. arenosa*, Spheniopsidae, Pandoridae, Periplomatidae

5.2.3 Analyses with restricted taxa

With the three taxa known only from shell material excluded from the dataset, analyses yielded 84 MPTs of length 179 and 181 with all characters treated as unordered and with three characters treated as ordered, respectively (CI = 0.40 and RI = 0.74 in both cases).

The two sets of MPTs produced identical strict consensus cladograms (Fig. 5.3), which were compatible with the majority-rule trees produced by analyses of the complete dataset. Compared to those majority-rule trees, the strict consensus produced by analyses of the reduced dataset resolves a clade joining Clavagelloidea to Laternulidae plus paraphyletic Lyonsiidae, but do not support nor reject the sister group relationships (1) of *Asthenothaerus maxwelli* with Cleidothaeridae, or (2) of *Thraciopsis angustata* and a clade joining *Myochama anomioides* with *Myadora brevis*. The former and latter relationships were suggested by 85 and 71% of the MPTs produced

by analyses of the pruned dataset, respectively.

Considering the congruence among results obtained with distinct parameters in effect, the strict consensus produced by analyses of the pruned dataset was chosen for character optimisation. Figure 5.4 plots character state transitions under the ACCTRAN algorithm and labels the clades discussed below.

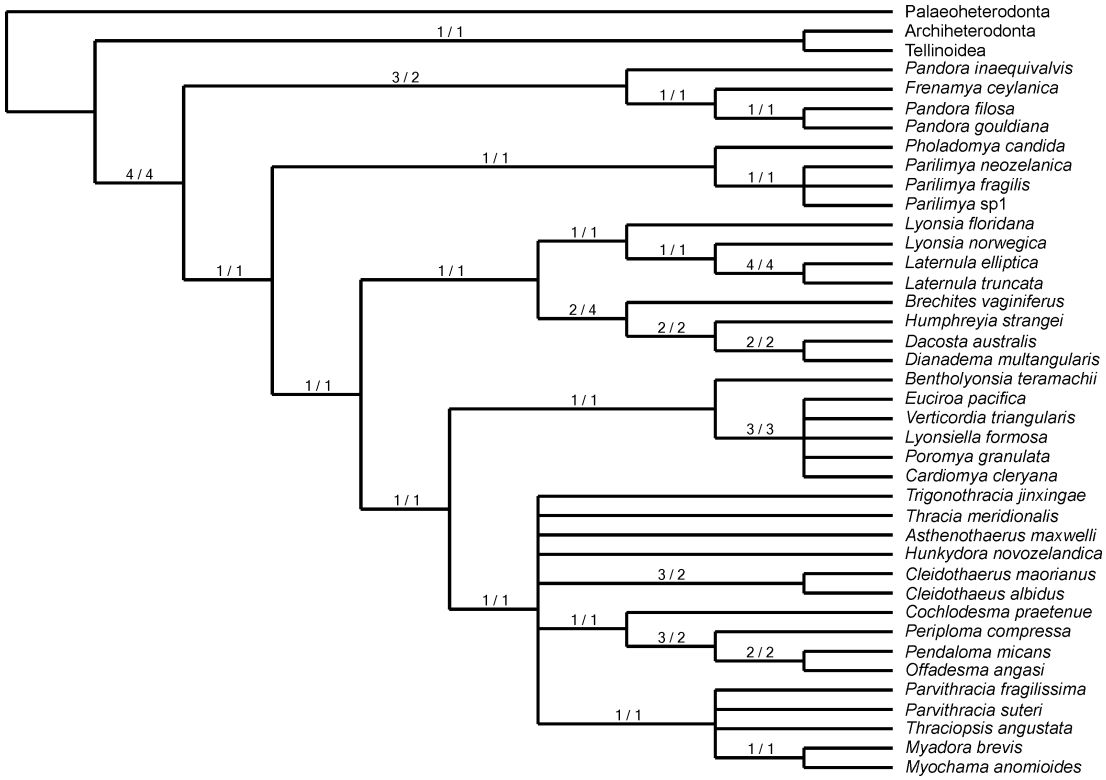


Figure 5.3: Strict consensus of MPTs recovered by analyses of the reduced dataset (*Grippina californica*, *Spheniopsis frankbernardi* and *Thracidora arenosa* excluded). Numbers above branches represent Bremer support index values with all characters treated as unordered (to the left of the slash) and with characters 5, 18 and 29 treated as ordered (to the right of the slash).

5.2.4 Clades and apomorphies

5.2.4.1 Clade A: Anomalodesmata

Monophyletic Anomalodesmata was recovered in all attempted analyses with relatively high branch support (Bremer's index values varying from 3 to 4). The most parsimonious reconstruction of character evolution on the cladogram in Figure 5.4 suggests loss of hinge teeth [characters 13, 14] and gains of plicated ctenidia, hermaphroditism and a thick encasing surrounding the eggs [characters 36, 58, 59] as unambiguous apomorphies of the group. These are features which have been long associated with representatives

of the clade (Dall, 1889*a*; Pelseneer, 1891*b*; Ridewood, 1903). A few other "typical anomalodesmatan characters" (Morton, 1985*a*) are ambiguously traced as supporting synapomorphies of the clade: loss of the ascending lamella of the outer demibranch [35], leading to ctenidia of type E (Atkins, 1937*b*), and insertion of the ventral tips of the inner demibranch unfused in the proximal oral groove [43], which characterises the category III of Stasek (1963*b*), are recovered as synapomorphies of Anomalodesmata under the DELTRAN optimisation (see Appendix C).

In addition to these foreseeable features, cuticular fusion between gills and body wall [40] was recovered as apomorphic for this clade under ACCTRAN optimisation, and both retention of a byssal apparatus into adulthood [47] and mantle fusion separating pedal from inhalant aperture [18] under DELTRAN. These are characters that have not been previously suggested as putative anomalodesmatan apomorphies.

5.2.4.2 Clade B: Pandoridae

Monophyly of Pandoridae was unanimously supported, regardless of the parameters in effect in individual trials. Except for analysis of the complete dataset with three ordered characters, which failed to resolve high-level relationships within Anomalodesmata (Fig. 5.3B), the family was always recovered as the most basal anomalodesmatan branch.

Pandorids are highly characteristic and comprise one of the only clades supported by non-homoplastic synapomorphies and with Bremer's support values of up to 3 in analyses of the dataset with "wildcard" taxa removed. The family is unambiguously supported by the exclusive discontinuous pallial line [8], crura [15] and pedal retractor muscles connecting to the shell ventral to the adductors [49]. It is also unambiguously supported by the path of the descending intestine [55], which runs postero-ventrally after leaving the crystalline style sac, a feature that has been independently evolved by several other lineages according to optimisation in the cladogram in Figure 5.4 (see Appendix C).

Ambiguous synapomorphies of Pandoridae are a long proximal oral groove [46] and an isolated duct from the digestive diverticula openning on the left side of the stomach, associated with the major typhlosole [52]. This duct was originally described by Allen (1954) in *Pandora inaequivalvis* but, unaware of Allen's (1954) paper and with only small specimens available for examination, Purchon (1958) failed to find it in the species. Because *P. inaequivalvis* was recovered as the most basal pandorid and is presently the only representative of the family whose stomach architecture has been studied in detail, ACCTRAN suggests this character as an apomorphy of the entire clade, whereas DELTRAN plots the duct as an autapomorphy of the species. Other

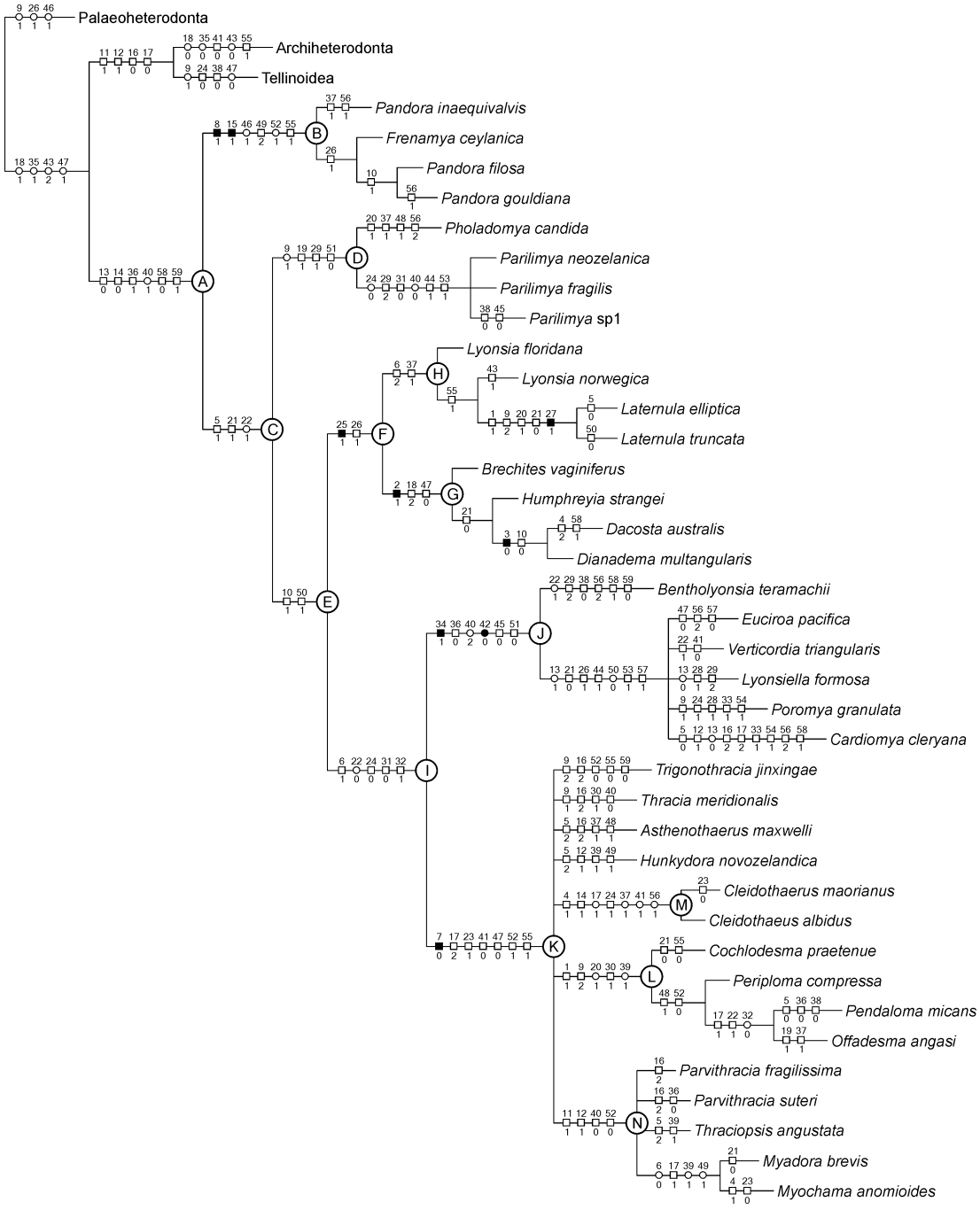


Figure 5.4: Character state transformations mapped on the strict consensus cladogram produced by analyses of the reduced dataset. Branches are depicted proportional to the branch length. Open and filled geometric forms indicate homoplastic and non-homoplastic character state transitions, respectively. Squares represent unambiguous transformations; circles indicate the ACCTRAN optimisation of characters which have alternative equally parsimonious solutions (see Appendix C). The numbers above and below the geometric forms denote characters and corresponding character states, respectively. Characters 5, 18 and 29 were treated as ordered. Letters in circles label clades discussed in the text.

autapomorphies of *P. inaequivalvis* are enlarged apical gill filaments [37] and rectum passing above the ventricle [56].

Within Pandoridae, a clade joining *Frenamya ceylanica*, *P. filosa* and *P. gouldiana* is unambiguously supported by well-developed siphonal tentacles [26], often occurring in multiple rows around the inhalant and exhant apertures, and the sister-group relationship of the two latter species by calcification of F1 into a solid lithodesma [10].

Autapomorphies are unknown for *Frenamya ceylanica* and *P. filosa*, whereas *P. gouldiana* is characterised by passage of the rectum above the ventricle [56], a putative parallelism with *P. inaequivalvis*.

5.2.4.3 Clade C

Clade C joins all extant anomalodesmatans but Pandoridae and is supported by three synapomorphies, two of which unambiguously optimised: calcified periostracal sculpture in the form of granules or spikes [5] and a fourth pallial aperture [21]. Additionally, arenophilic glands [22] are traced as an apomorphic feature of this clade under the ACCTRAN reconstruction.

These three features are normally considered typical of anomalodesmatans as a whole and their absence in pandorids, recovered herein as plesiomorphic, traditionally interpreted as secondary losses.

5.2.4.4 Clade D: Pholadomyoidea

Monophyletic Pholadomyoidea was represented in 60% of the shortest trees produced by analysis of the complete dataset with three ordered characters, and unanimously supported by MPTs produced in the remaining three analyses. The clade has low branch support (Bremer's index of 1) and a maximum of 5 synapomorphies.

A wide ventral mantle margin in between left and right periostracal grooves [19], a pair of hypertrophied muscular bundles inserted to the shell among the remaining siphonal retractors muscles [29] and loss of lateral grooves in the internal oesophageal wall [51] are unambiguously reconstructed as synapomorphies of Pholadomyoidea, whereas arenophilic glands [22] and a parivincular ligament representing F2 [9] are traced as such under DELTRAN alone and both ACCTRAN and DELTRAN, respectively.

Within Pholadomyoidea, *Pholadomya candida* appears as the sister-group to monophyletic Parilimyidae, the latter clade being apomorphically characterised by hypertrophied siphonal retractors gaining a separate insertion area on the shell wall [29], loss of a central band of circular musculature in the siphonal walls [31], reduced labial palps [44] and a muscular stomach [53]. Loss of pallial pigmentation [24] and reversal from

cuticular to cilliary connection between gills and body wall [40] might represent other synapomorphies of parilimyids but these characters, recovered as such under ACCTRAN, have equally parsimonious alternative optimisations. Relationships within Parilimyidae are unclear.

Among pholadomyoids, autapomorphies were only unambiguously recovered for *Pholadomya candida* and *Parilimya* sp1.

The former species displays four features traced as apomorphic in the present analysis, namely orbital muscles [20], apical filaments [37], opisthopodium [48] and rectum passing below the ventricle [56]. In addition to these homoplastic attributes, *P. candida* bears at least one organ which is unknown in other anomalodesmatans, a pair of muscular bundles with proximal and distal ends inserted on opposite valves, which cross the commissural plane in front of the pedal aperture (Morton, 1980).

Parilimya sp1 is characterised by two autapomorphies presumably related to its feeding habits: loss of the ctenidial marginal food groove [38] and loss of sorting ridges on the oralward surfaces of the labial palps [45].

5.2.4.5 Clade E

Clade E joins all thracioids, clavagelloids and septibranchs plus representatives of all families traditionally grouped under Pandoroidea but pandorids. In the analysis with all scored taxa included and characters treated as unordered, the poorly known *Thracidora arenosa*, *Grippina californica* and *Spheniopsis frankbernardi* also clustered here.

Only two synapomorphies, calcification of F1 into a lithodesma [10] and occurrence of several statoconia in each statocyst [50], are unambiguously traced to this clade. With DELTRAN in effect, transition from cilliary to cuticular connection between gills and body wall [40] is also reconstructed as a synapomorphy of clade E.

5.2.4.6 Clade F: Lyonsiidae + Laternulidae + Clavagelloidea

The grouping of lyonsiids, laternulids and clavagelloids was recovered only in analyses of the reduced dataset and is supported by two unambiguous synapomorphies relating to siphonal morphology: periostracal grooves positioned at the apex of the siphons, resulting in an external coat of periostracum over the external siphonal walls [25] and tentacles bearing an apical ciliated pit, often organised in multiple rows around inhalant and exhalant apertures [26].

Under DELTRAN optimisation, arenophilic glands [22] are also traced as a synapomorphy of this clade.

5.2.4.7 Clade G: Clavagelloidea

Clavagelloidea was recovered as a clade in all attempted analyses, with Bremer's support values varying from 1 (entire dataset with all characters treated as unordered) to 4 (reduced dataset with three ordered characters).

Unambiguous synapomorphies of the group are the crypt with at least one valve fused to the wall [2], which is unique among bivalves, ventral mantle fusion involving left and right periostracal grooves [18] and adults either completely devoid of a byssal apparatus or displaying only a tiny groove at the heel of the foot, without signs of an associated gland in histological sections [47].

Within Clavagelloidea, the cementing *Humphreyia strangei* forms a clade with *Clavagella australis* and *Dianadema multangularis*, supported only by loss of the adult fourth pallial aperture as an unambiguous synapomorphy [21]. Grouping of these three taxa renders *Brechites vaginiferus* a functional outgroup for polarisation of character 3 (whether the crypt is secreted by one or both mantle lobes), applicable only within Clavagelloidea. Together with loss of a lithodesma [10], secretion of the crypt by the left mantle lobe alone [3] was thus recovered as unambiguous synapomorphies of the family Clavagellidae, represented in the present analyses by *Clavagella australis* and *Dianadema multangularis*.

Autapomorphic character transitions were only reconstructed in *Clavagella australis*, which cements to hard substrata by the left valve [4] and is unusual among anomalodesmatans for being apparently dioecious [58] (Morton, 1984*a*).

5.2.4.8 Clade H: Lyonsiidae + Laternulidae

A clade joining lyonsiids and laternulids was found in the analysis of the complete dataset with all characters treated as unordered and in both searches with "wildcard" taxa excluded, although never with Bremer's index of branch support superior to 1 step.

Two unambiguous synapomorphies were recovered for this clade: calcified periostracal elements absent or fading posterior to the diagonal ridge [6] and enlarged apical filaments in each ctenidial plicae [37].

Monophyly of Lyonsiidae is rejected because representatives of the type genus appear as successive sister-groups of monophyletic Laternulidae. The latter family is well-characterised and bears the largest values of branch support recovered in the present analyses, with 3 to 4 extra steps being required to lose the clade from the strict consensus cladogram, depending on the parameters in effect. Its unambiguous synapomorphies are: umbonal slit [1], disjunct ontogeny of fibrous ligament, with F2

supported by chondrophores [9], orbital muscles [20], loss of a fourth pallial aperture [21], and complex eyes, unique among anomalodesmatans [27].

Laternula elliptica and *L. truncata* are autapomorphically characterised by loss of periostracal calcification [5] and reversal of numerous statoconia to a single statolith per statocyst [50], respectively.

Grouping of *Lyonsia norwegica* with Laternulidae is supported by only one unambiguous synapomorphy: an anterior loop taken by the descending intestine before travelling towards the pericardial cavity [55].

In *Lyonsia norwegica* the ventral tip of the inner demibranch is fused to the proximal oral groove, a feature recovered as autapomorphic in the present analyses, but previously reported in *L. californica* by Narchi (1968). No autapomorphies were reconstructed along the branch leading to *Lyonsia floridana*.

5.2.4.9 Clade I

This large clade, which joins septibranchs, thraciids, periplomatids, myochamids and cleidothaerids, was recovered in strict consensus trees only following the exclusion of "wildcard" taxa. Despite its low support (Bremer's index of 1), four unambiguous synapomorphies are reconstructed along its branch: calcified periostracal elements coarser posterior to the diagonal ridge [6], nerve cords running along the hemocoelic space of the siphonal walls [32] and losses of pallial pigmentation [24] and central circular muscular layer of the siphons [31]. In addition to these, loss of arenophilic glands [22] is traced to this clade under ACCTRAN optimisation.

5.2.4.10 Clade J: Septibranchia

Septibranchs have been traditionally regarded as highly distinctive and, accordingly, synapomorphies recovered for this clade depart little from the lists of characteristic features of the group compiled by previous investigators (Ridewood, 1903; Morton, 1985*a*). Change in alignment of the gills from parallel to perpendicular to the commissural plane [34] and losses of ctenidial plication [36], sorting ridges on the labial palps [45] and lateral grooves in the oesophagus [51] were unambiguously traced to the septibranch branch, whereas attachment of the gills to the body wall by tecidual junctions [40] and loss of interlamellar septa [42] are recovered under ACCTRAN.

Relationships among septibranchs are poorly resolved in the strict consensus, as only one node splitting the lyonsiellid *Bentholyonsia teramachii* from the other 5 sampled species was present in all MPTs. Branch support for this grouping of 5 septibranchs was relatively high, with Bremer's index values of 3 in both analyses of the reduced dataset.

With this large polytomy interpreted as an event of multiple speciation, five synapomorphies are unambiguously traced to its branch: loss of a fourth pallial aperture [21], conspicuous tentacles with an apical ciliated pit and generally organised in multiple rows, surrounding inhalant and exhalant apertures [26], reduced labial palps [44], posterior wall of the stomach expanded into a muscular sac [53], and kidneys extending laterally into the mantle [57].

A conspicuous tooth tentatively homologised with a heterodont cardinal is present in the right valve of *Euciroa pacifica*, *Verticordia triangularis* and *Poromya granulata* but not in the other two species involved in the polytomy. Hence, ACCTRAN places gain of this tooth along the branch leading to the polytomy, followed by two reversals [13], whereas DELTRAN favours three independent derivations of this tooth, one in each of the species listed above.

Another character of ambiguous optimisation for the polytomy as a whole is the number of masses in each statocyst capsule. This feature has been studied only in *Poromya granulata* (Pelseneer, 1891*a*; Morton, 1981*c*) and *Cardiomya cleryana* (this study) among taxa involved in the polytomy. *C. cleryana* has a single statolith per statocyst but in *P. granulata* Pelseneer (1891*a*) described two to three statoconia in each capsule and Morton (1981*c*) a single statolith. Because literature data for *P. granulata* is conflicting, this species was ascribed missing data for this character in the present dataset. With only *C. cleryana* coded, transition from several statoconia to a single statolith is deemed a synapomorphy of the entire polytomy under the ACCTRAN optimisation, whereas DELTRAN plots this transformation as an autapomorphy of the species.

Autapomorphies were reconstructed for all six septibranchs included in the analysis, although some might prove to represent synapomorphies pending resolution of septibranch interrelationships.

For *Bentholyonsia teramachii*, hypertrophied siphonal retractors with a separate insertion area on the shell wall [29], loss of the marginal food groove of each inner demibranch [38], rectum passing below the ventricle [56], dioecious reproduction [58] and loss of the capsule surrounding eggs [59] were unambiguously optimised, whereas gain of arenophilic glands [22] was traced under ACCTRAN and DELTRAN.

Unambiguous autapomorphies for *Euciroa pacifica* were loss of byssal apparatus in adults [47], rectum passing below the ventricle [56] and loss of kidneys extending laterally into the mantle [57].

Verticordia triangularis is apomorphically characterised by gain of arenophilic glands [22] and transition from tecidual to ciliary connection between left and right inner demibranchs, posterior to the visceral mass [41].

Autapomorphies recovered for *Lyonsiella formosa* are a siphonal cowl [28] and hypertrophied siphonal retractors with a separate insertion area on the shell wall [29].

Five autapomorphies were unambiguously recovered for *Poromya granulata*: disjunct ontogeny of fibrous ligament with F2 supported by nymphs [9], pallial pigmentation [24], siphonal cowl [28], gills modified into a muscular septum [33] and style sac separated from midgut [54].

The two latter character state transformations were also retrieved as unambiguous autapomorphies of *Cardiomya cleryana*, together with loss of periostracal calcification [5], a posterior lateral tooth on the right valve [12], transition of the middle and inner shell layers from nacreous to fine grained microstructures [16, 17], rectum passing below the ventricle [56] and dioecious reproduction [58].

5.2.4.11 Clade K: Thraciidae + Periplomatidae + Myochamidae + Cleidothaeridae

This clade was recovered only in analyses of the reduced dataset and with low branch support. The most parsimonious reconstruction of character state transformations in Figure 5.4 suggests seven synapomorphies for this grouping: loss of radial alignment of the calcified periostracal ornamentation on the external surface of the shell [7], microstructure of the inner shell layer transitioning from nacreous to a fined grained fabric resembling crossed lamellar [17], modification of part of the internal surface of the right mantle lobe into a tall, columnar and glandular epithelium [23], connection between left and right inner demibranchs posterior to the visceral mass shifting from tecidual to ciliary [41], byssal apparatus either completely lacking or represented only by a tiny groove with no associated gland in adults [47], isolated duct from the digestive diverticula opening on the left wall of the stomach in association with the major typhlosole [52] and an anterior loop described by the descending intestine before travelling toward the pericardial cavity [55].

Internal relationships among components of this clade are poorly resolved in the strict consensus, but its topology supports Cleidothaeridae and Periplomatidae as monophyletic groups. Monophyly of Thraciidae and Myochamidae is rejected because representatives of *Parvithracia* and *Thraciopsis*, genera traditionally referred to the former family, cluster with a clade of myochamids, whereas the remaining sampled terminals of these two families (thraciids *T. jinxingae*, *T. meridionalis* and *A. maxwelli*; myochamid *H. novozelandica*) appear involved in a large basal polytomy.

With this polytomy interpreted as an event of multiple speciation, autapomorphies reconstructed for *T. jinxingae* were: disjunct adult ligament, with F2 supported by chondrophores [9], microstructure of the middle shell layer shifting from nacreous to

fine-grained [16], modification of the digestive tract involving losses of the isolated duct from the digestive diverticula and anterior loop of the descending intestine [52, 55] and loss of a capsule encasing eggs individually [59].

Autapomorphies traced to *T. meridionalis* also included microstructure of the middle shell layer transitioning to fine-grained [16] and a disjunct ligament, but with F2 supported by nymphs instead of chondrophores [9]. The most parsimonious reconstruction also suggested the formation of mucus-lined siphonal galleries [30] and connections between gill and body wall shifting from cuticular to ciliary [40] as additional autapomorphies of *T. meridionalis*.

Transition of granular or spicular to brick-shaped calcified periostracal elements [5] was traced as autapomorphies of both *A. maxwelli* and *Hunkydora novozelandica*. Additionally, the former species is apomorphically characterised by fine-grained microstructure in the middle shell layer [16], apical filaments [37] and opisthopodium [48]. The latter has the autapomorphies: posterior lateral tooth in the right valve [12], tentacular appendixes projecting from the inter-siphonal septum [39] and posterior pedal retractors attaching to the shell among fibres of the posterior adductor [49].

5.2.4.12 Clade L: Periplomatidae

This subgroup of clade K was retrieved with identical topology among terminals and low branch support in all attempted analyses. Its suggested synapomorphies include two shell features that have been traditionally used as a diagnostic character linking periplomatids to laternulids but which were found homoplastic herein: umbonal slit [1] and adult ligament supported by conspicuous chondrophores [9]. In addition to these attributes, mucous lining of the siphonal passages through the sediment [30] was unambiguously traced as a synapomorphy of the family, and both orbital muscles [20] and a pair of tentacular appendixes projecting from the inter-siphonal septum [39] reconstructed as such under ACCTRAN.

Relationships among sampled periplomatids are fully resolved and relatively well supported (Bremer's index values varying from 2 to 3). *Cochlodesma praetenue* constitutes the sister-group of *Periploma compressum* + *Pendaloma micans* + *Offadesma angasi*, a clade apomorphically characterised by presence of an opisthopodium [48] and loss of an isolated duct from the digestive diverticula opening on the left wall of the stomach [52]. Characters 20 and 39, reconstructed under ACCTRAN as synapomorphies of Periplomatidae, are traced to this subgroup under DELTRAN because their state is unknown in *C. praetenue*.

Analyses suggested *Pendaloma micans* and *Offadesma angasi* are more closely related to one another than they are to *Periploma compressum*, with the supporting

synapomorphies: arenophilic glands [22] and reversal of fine grained to nacreous microstructure in the inner shell layer [17]. Additionally, *Offadesma angasi* has siphonal nerves running along the internal layer of longitudinal musculature [32], whereas conditions of this character in *Pendaloma micans* are currently unknown. Hence, ACCTRAN optimisation plots this feature as a synapomorphy of the two species, whereas DELTRAN favours an autapomorphic transition in *Offadesma angasi*.

Autapomorphic transformations were unambiguously reconstructed in all periplomatid terminals, except *Periploma compressum*.

Cochlodesma praetenue bears the autapomorphic losses of a fourth pallial aperture [21] and of the anterior loop of the descending intestine [55].

Three other losses are traced to *Pendaloma micans*: of periostracal calcification [5], ctenidial plication [36] and marginal food groove [38].

Finally, the most parsimonious reconstruction of character state changes traces two unambiguous autapomorphies to *Offadesma angasi*: wide ventral mantle margins between left and right periostracal grooves [19] and enlarged apical filaments in each ctenidial plica [37].

5.2.4.13 Clade M: Cleidothaeridae

Monophyletic Cleidothaeridae was recovered in all attempted analyses, with values of Bremer's support index varying from 1 (complete dataset with three ordered characters) to 3 (restricted dataset with all characters treated as unordered). This is unsurprising because the two nominal species of *Cleidothaerus* included in the present analyses are so similar they have been considered synonyms by several authors (see discussion in Morton, 1974). Although the two terminals coded herein differ in the presence of pallial glands in the right mantle lobe, Morton & Harper (2001) suggested these organs are a source of cement in *C. albidus* and hence their apparent absence in *C. maorianus* might be because the specimen analysed histologically by Morton (1974) had ceased to cement.

The most parsimonious reconstruction of character state transitions suggests as synapomorphies of Cleidothaeridae: cementation to hard substrata by the right shell valve [4], cardinal tooth on the left valve [14] and pigmentation of the mantle margins [24]. In addition to these unambiguously optimised features, transition of the microstructure of the inner shell layer from fine-grained to nacreous [17], enlarged apical filaments in each ctenidial plica [37], transition from ciliary to cuticular connection between left and right inner demibranchs [41] and rectum passing above the heart [56] are known only in one of the two sampled species of *Cleidothaerus*. Hence, they are

plotted either as synapomorphies of the family or autapomorphies of the species in question under ACCTRAN and DELTRAN optimisations, respectively (see Appendix C).

5.2.4.14 Clade N: Thraciidae (part) + Myochamidae (part)

This clade, which joins taxa traditionally placed in the families Thraciidae and Myochamidae, was recovered only in analyses of the reduced dataset, with low branch support.

Four character state transformations were unambiguously traced as synapomorphies of this grouping: anterior and posterior lateral teeth on the right valve [11, 12], connection between gills and body wall shifting from cuticular to ciliary [40] and loss of an isolated duct from the digestive diverticula opening on the left side of the stomach in association with the major typhlosole [52].

Within the clade, the only sister-group relationship present in all MPTs is that of the myochamids *Myadora brevis* and *Myochama anomioides*, supported by only one unambiguous synapomorphy, namely microstructural transition of the inner shell layer from fine-grained to nacreous [17]. *M. brevis* displays a number of additional features which, previously to the present study, had not been described or given systematic value. For this reasons, the state of these characters have not been noted in literature accounts of *M. anomioides* (Hancock, 1853*b*; Harper & Morton, 2000) but may nevertheless also characterise that species. These attributes, which are traced as synapomorphies of the two myochamids or autapomorphies of *M. brevis* under ACCTRAN and DELTRAN respectively, are: uniform size of calcified periostracal elements throughout the dissoconch [6], paired tentacular projections of the intersiphonal septum [39] and posterior pedal retractor attached to the shell in the middle of the posterior addutor [49].

Unambiguous autapomorphies were reconstructed for all terminals in clade N. Both *Parvithracia* species are apomorphically characterised by fine grained microstructure in the middle shell layer, and *P. suteri* has smooth ctenidia, without plicae, as an additional autapomorphy [36]. In *Thraciopsis angustata* calcified periostracal elements change morphology, becoming brick-shaped [5] and paired tentacular projections of the intersiphonal septum are gained [39]. Loss of the fourth pallial aperture [21] is traced as the only autapomorphy of *M. brevis*. Suggested autapomorphies of *M. anomioides* are cementation to hard substrata by the right shell valve [4] and loss of pallial glands on the right mantle lobe [23].

5.3 Discussion

5.3.1 Character fit

In all four attempted analyses the consistency index of resulting most parsimonious trees was rather low (ranging from 0.39 to 0.40), suggesting that anomalodesmatan evolution has been highly homoplastic, with several instances of parallelisms, convergences and secondary losses of morphological traits. This is not unexpected, considering that bivalves in general are often cited as epitomes of homoplastic evolution (e.g. Stanley, 1970, 1975; Newell & Boyd, 1978; Boss, 1978; Seilacher, 1984). Indeed, consistency indexes for bivalve cladograms are typically low (e.g. Roopnarine, 1996; Schneider, 1998*a*; Harper *et al.*, 2000; Tëmkin, 2006) and the perceived high incidence of homoplasy in the group has contributed to the delayed adoption of cladistic methods by bivalve systematicians (see Schneider, 2001, for a review).

Values of the retention index were much higher (0.74 in all analyses), indicating that despite displaying extra steps, most characters represented synapomorphies of recovered clades and thus retained evidential value.

5.3.2 Suggested relationships

Cladograms recovered by the present analyses corroborate monophyly of a number of families suggested by authoritative treatments of anomalodesmatan systematics, as well as some of the groupings proposed by the conflicting cladistic studies of Boss (1978), Harper *et al.* (2000, 2006) and Dreyer *et al.* (2003). However, they also suggest a number of relationships not previously advocated, the most surprising being the position of Pandoridae as the most basal anomalodesmatan clade and recovery of Periplomatidae relatively distant from Laternulidae. These and other implied relationships are discussed in the sections below.

5.3.2.1 *Thracidora arenosa* and Spheniopsidae

T. arenosa is a poorly known Australian species whose systematic placement is controversial. It was originally described by Hedley (1904) as a representative of the thraciid genus *Thraciopsis*. Subsequently, it was transferred to a genus of its own by Iredale (1924) who considered the species too different from *Thraciopsis angustata*, the type species of *Thraciopsis*, to keep both under the same generic name. Thiele (1935, translated by Bieler & Mikkelsen, 1998), Soot-Ryen (1966) and more recently Prezant (1998*e*) treated the genus under Lyonsiellidae rather than Thraciidae, but offered no justification for this taxonomic decision. In a comprehensive treatment Lyonsiellidae, Allen & Turner (1974) expressed the opinion that *Thracidora* more closely resembles

members of the Thraciidae and Myochamidae for having an elongated and compressed shell with subcentral umbones.

In the present study, analyses of the complete dataset placed the species in the sister-group of Pholadomyoidea but failed to resolve its relationships further, neither supporting nor rejecting the conflicting views summarised above.

Spheniopsidae, a family traditionally considered to have myoid affinities, was recently referred to Anomalodesmata by Marshall (2002), who commented on similarities shared by the spheniopsid genus *Grippina* and anomalodesmatans of the families Thraciidae and Cuspidariidae.

The present analyses recovered Spheniopsidae as an anomalodesmatan family, with most MPTs suggesting its placement in a clade also comprising thraciids and myochamids (clade N), a result which apparently supports Marshall's (2002) opinion. However, the only character states shared by spheniopsids and representatives of clade N which are not also shared by the outgroups are the absence of cardinal teeth and fine grained shell microstructure. These are features which characterise several other heteroconch outgroups, particularly myoids, and it is therefore uncertain whether the placement of Spheniopsidae suggested by Figure 5.2 may be reproduced in analyses counting with a larger selection of outgroup taxa.

5.3.2.2 Pandoridae

Pandorids have been traditionally regarded as allied to lyonsiids, and a more or less close relationship between these families was found in previous cladistic analyses of extant anomalodesmatans, with either morphological or molecular datasets (Fig. 5.5A–C; Harper *et al.*, 2000, 2006).

The position of the family recovered in the present investigation is not only incompatible with every hypothesis of anomalodesmatan phylogeny to date, but also with the fossil record of the group. Because the pholadomyoid genus *Pholadomya* had appeared by the Upper Triassic (Carnian), whereas the first recognised pandorid is known from rocks of Eocene (Ypresian) age (Skelton & Benton, 1993; Sepkoski, 2002), placing the latter family in a more basal position than the former would imply a gap of more than 150 million years in the fossil record of pandorids.

Instead, it seems more likely that the position of Pandoridae in cladograms recovered by the present analyses does not reflect the sister-group relationships of this family. Such failure seems attributable to two main factors: (1) morphological characters that could link Pandoridae to the sister-groups suggested by previous investigators (particularly in molecular trees) are difficult to code in meaningful discrete states and have been excluded from the present dataset; and (2) if the position of the family depicted in

previous cladograms are a good approximation of its true relationships, then it is clear that pandorids have secondarily lost many of the anatomical features that are typical of anomalodesmatans.

With regard to the first point, among other less obvious features pandorids share with lyonsiids a shell of overall similar shape, with the left valve larger and more convex than the right, posterior end elongated into a rostrum and gills normally extending well past the posterior adductor muscle into the proximal region of the short siphons. Gills extending into the siphons are also shared by laternulids and clavagelloids, taxa that are related to pandorids and lyonsiids according to molecular data (Harper *et al.*, 2006). Although these features may be potentially useful sources of phylogenetic signal, they display continuous variation within Anomalodesmata and hence require calculated confidence intervals around mean values for their appropriate cladistic treatment (Farris, 1990; Goloboff *et al.*, 2006). Due to lack of specimens and reliance on literature accounts as sources of data for several terminals, these and all other continuous characters were excluded from the present dataset.

And with concern to the second point, rather than constituting synapomorphies of all other extant anomalodesmatans (Clade C), primitively absent in pandorids, it seems more likely, at least in the author's mind, that periostracal calcification, a fourth pallial aperture and arenophilic glands were secondarily lost in Pandoridae. Significantly, these characters seem particularly prone to homoplasy, displaying a consistency index considerably lower than the average of 0.4 recovered for the entire dataset (0.16 for fourth pallial aperture, 0.2 for arenophilic glands and 0.28 for periostracal calcification).

Calcification of the mid-sagittal sector of the ligament into a solid lithodesma, a character recovered as a synapomorphy of the sister-group of Pholadomyoidea (Clade E, within which Pandoridae has been recovered in previous studies; Fig. 5.5), is similarly lost in several but not all pandorids, and was optimised as primitively absent in the family. However, if the interpretation of the functional significance of the lithodesma given by Yonge (1976) and expanded in section 2.3.4 can hold, secondary loss of the ossicle in pandorids may be a consequence of their typically very compressed shells in which the distance between left and right resilifers is small enough to maintain an appropriate width to cross-sectional ratio of the ligament throughout ontogeny.

5.3.2.3 Pholadomyoidea

Although a close relationship between parilimyids and septibranchs has been suggested (Morton, 1982), cladograms recovered herein concur with those of Harper *et al.* (2000) in supporting monophyly of Pholadomyoidea. The basal position of the superfamily is unsurprising and corroborates the long held view that it represents the most plesiomor-

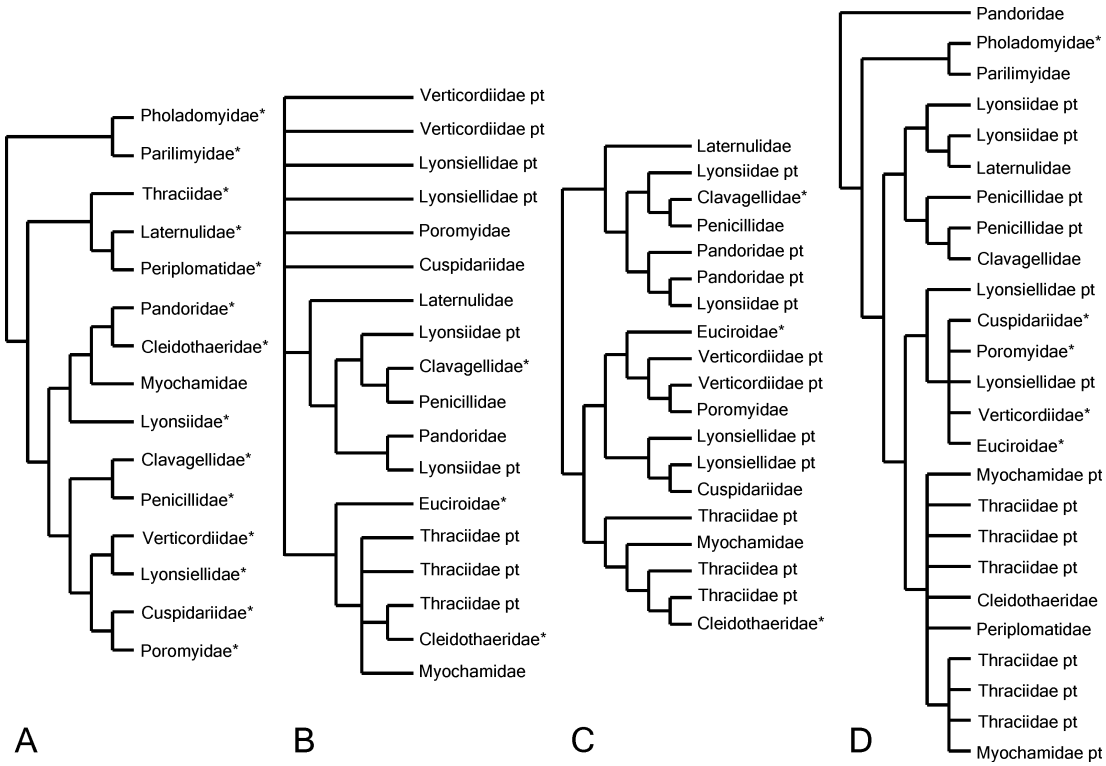


Figure 5.5: Comparison of cladograms depicting the relationships of extant anomalodesmatan families, produced by the morphological study of Harper *et al.* (2000) (**A**), molecular analyses of Harper *et al.* (2006) with tree searches unconstrained (**B**) or constrained for monophyletic Septibranchia (**C**) and the present analyses with "wildcard" taxa excluded (**D**). Families recovered as non-monophyletic are indicated by "pt" and those represented by only one terminal in each analysis (monophyly untested) by an asterisk after their name.

phic extant anomalodesmatan group (Pojeta, 1971; Runnegar, 1974), on the basis of which Harper *et al.* (2000) selected the taxon as an outgroup in their analysis.

Monophyly of Parilimyidae has been tested for the first time in a cladistic context because analyses by Harper *et al.* (2000) included only one terminal of the family and, as commented above, pholadomyoids have not yet been included in molecular studies.

Characters shared by parilimyids and some septibranchs which led (Morton, 1982) to infer a carnivorous diet in *Parilimya fragilis*, namely reduced labial palps, taenioid muscles with separate insertions on the shell wall and posterior wall of the stomach expanded into a muscular sac, were unambiguously optimised as convergences in the present analyses.

5.3.2.4 Pandoroidea sensu Newell *et al.*

Monophyly of a group uniting the families Pandoridae, Lyonsiidae, Cleidothaeridae, Myochamidae, Thraciidae, Periplomatidae and Laternulidae had been little contentious

in pre-cladistic revisions of the Anomalodesmata (e.g. Morton, 1981*b*, 1985*a*; Prezant, 1998*b*) and considered valid in Boss' (1978) early cladistic study. However, it was rejected by both morphological and molecular cladistic surveys of the group (Fig. 5.5A–C). The present analyses echoes these findings and, by tracing state transitions of characters traditionally cited in support of this grouping, helps to explain why it is probably polyphyletic.

All cladograms in Figure 5.5 render Pandoroidea sensu Newell *et al.* (1969*b*) non-monophyletic because clavagelloids and septibranchs appear nested within the group. The latter two groups are highly characteristic and have been attributed superfamilial status for displaying features that are exclusive not only among anomalodesmatans but also bivalves as a whole, namely the crypt with part of the shell visible from the outside and the unusual configuration of the gills (non-homoplastic synapomorphies indicated in Figure 5.4).

As for Pandoroidea sensu Newell *et al.* (1969*b*), Keen (1969*b*) cites in the diagnosis featured in the *Treatise* a burrowing habit, nacreous inner shell layer, inequivalve shells, edentulous hinge and a lithodesma, whereas Runnegar (1974) defined the group as comprising all anomalodesmatan genera with an internal ligament supported by a lithodesma. Boss (1978, p. 420) gives the most comprehensive diagnosis of the superfamily:

> "The following features are shared by the constituent families at the superfamilial level, a lineage represented by the ancestral laternulids in the Triassic: shell aragonitic, tri-layered, prismato-nacreous; hinge with opisthodetic external element and variously developed internal resilial element subtended by an accessory calcareous structure, the lithodesma; shell often invested with granules; animal siphonate, mantle fused ventrally except for the antero-ventral pedal aperture, subsiphonal postero-ventral, so-called fourth pallial aperture, and posterior incurrent and excurrent siphons; foot provided with byssal groove; ctenidia consisting of ventrally pendant inner demibranch with both ascending and descending lamellae and of dorsally reflected outer demibranch with only descending lamellae; palp-ctenidial relation type III of Stasek; stomach of Purchon's type IV and Dinamani's type IIIB; animal reproductively hermaphroditic."

Except for the lithodesma and inequivalve shell, all listed features are shared with pholadomyoids and several also characterise other heterodonts, being therefore plesiomorphies. And with regard to inequivalve shells and a lithodesma, numerous septibranchs and clavagelloids display these features and it is significant in this sense that

the latter organ was unambiguously traced as a synapomorphy of clade E in the present study.

Hence, Pandoroidea sensu Newell *et al.* (1969*b*) is a group of convenience for representatives of clade E lacking the apomorphic features of clavagelloids and septibranchs.

5.3.2.5 Pandoroidea and Thracioidea sensu Boss

As explained in more detail in section 1.2.2, division of Pandoroidea sensu Newell *et al.* (1969*b*) into two superfamilies, one comprising Pandoridae, Lyonsiidae, Cleidothaeridae and Myochamidae and the other Thraciidae, Periplomatidae and Laternulidae had been hardly questioned before publication of the molecular studies of Dreyer *et al.* (2003) and Harper *et al.* (2006). Molecular cladograms produced by the latter authors recovered two monophyletic groups involving pandoroids and thracioids (Fig. 5.5): (1) a group which they termed "lyonsiid clade", joining Lyonsiidae, Laternulidae, Clavagelloidea and Pandoridae, with all but the first taxon recovered as monophyletic; and (2) a "thraciid clade" grouping Thraciidae, Cleidothaeridae, and Myochamidae, with the last family recovered as monophyletic.

Boss (1978, p. 420), who is responsible for the split between Pandoroidea and Thracioidea, identified a number of features deemed apomorphic in support of his decision: "Synapomorphic characters for the thraciid-laternulid-periplomatid lineage include elongate siphons, pallial sinus distinct and large, ventral pallial adductor muscles, ligament supported by nymphal callosity or chondrophores. In contrast, the remaining four families share a nearly opposing matrix of derived characters: comparatively short siphons with a concomitant reduction or absence of a pallial sinus, and a sunken resilium which is not supported by specialised structures such as a chondrophore"

The morphological analysis of Harper *et al.* (2000) supported monophyly of these two superfamilies and the most parsimonious reconstruction of character evolution on their "total evidence tree" (Harper *et al.*, 2000, fig. 2), traces the following unambiguous synapomorphies to each of the two taxa (Sartori, personal observations): (1) Thracioidea: adhesion of foreign material to shell exterior (Harper *et al.*, 2000, character 2), ligament sunken between chondrophores (char. 10), loss of fourth pallial aperture (char. 15) and rectum penetrating kidneys (char. 36); (2) Pandoroidea: ligament simple sunken (char. 10) and presence of sorting surfaces on the stomach (char. 34).

Boss (1978) regards as synapomorphies of each taxon alternative manifestations (states) of the same characters and it is therefore apparent that for each character being compared one of the superfamilies displays a plesiomorphic condition. Elongated siphons and large pallial sinus are dependent characters, display continuous variation within the group (hence their exclusion from the present study) and, if they are apo-

morphic for thracioids, as suggested by Boss (1978, p. 420), then the short siphons without pallial sinus of pandoroids must be plesiomorphic rather than part of "a nearly opposing matrix of derived characters". The same criticism applies to ligament structure — adult ligament supported by nymphs is plesiomorphic for anomalodesmatans whereas a sunken resilium not supported by specialised structures is also shared by most clavagelloids and septibranchs. Besides, as noted by Dreyer *et al.* (2003) many if not all of these characters are linked to depth of burial so that their sharing between taxa may indicate convergence of life habit rather than phylogenetic proximity.

Significant problems may be also pointed out in the synapomorphies recovered by analysis of Harper *et al.*'s (2000) data:

1. Adhesion of foreign material to the shell exterior may be brought about by several non-homologous mechanisms (e.g. Allen, 1960*b*; Braithwaite *et al.*, 2000) and, although in anomalodesmatans the process is often mediated by secretion from arenophilic glands, scoring of the character reported by Harper *et al.* (2000, appendix 2) does not correspond to the taxonomic distribution of the organs, which were treated as a separate character anyway (their character 14).

2. Being the only species traditionally classed in Thraciidae whose anatomy had been studied in detail, *Trigonothracia jinxingae* was used by Harper *et al.* (2000) as the only data source for scoring the family. The second and third putative synapomorphies of Thracioidea recovered by optimisation of their characters (ligament sunken between chondrophores and loss of the fourth pallial aperture) are direct results of this restriction in taxonomic sampling. As explained in detail in section 2.4.1, taxa traditionally classed in Thraciidae display a wide array of distinct ligament architectures which include not only species with chondrophores such as *T. jinxingae*, but also with typical nymphal ridges or a "simple sunken" internal ligament with mid-sagittal lithodesma. Similarly, a fourth pallial aperture is apparently absent in *T. jinxingae* but characterises most thraciids.

3. In most bivalves the rectum penetrates the pericardial cavity and passes above the kidneys and posterior adductor muscle before terminating at the anus. Along part of this trajectory, the rectum may be enveloped by left and right protuberances from the kidneys to varying degrees (see, for example, Sartori & Domaneschi, 2005, fig. 13). In some taxa these protuberances may meet at the commissural plane dorsal to the rectum, giving the impression that the intestine effectively penetrates the kidneys. However, variation in the extent of these lateral projections of the kidneys appear continuous and the opinion that they are more developed in thracioids than other anomalodesmatans does not seem defensible.

4. Sorting surfaces are typically present on the internal walls of the stomach of microphagous bivalves and within Anomalodesmata have been considerably reduced, albeit still present, only in septibranchs. Presence of the sorting ridges is therefore plesiomorphic within Anomalodesmata.

Hence, there seems to be little grounds to justify the status of Pandoroidea and Thracioidea sensu Boss (1978) as natural groups. Analyses undertaken herein rejected monophyly of these traditional superfamilies and recovered instead two clades (F and K) which, with the exception of absence of Pandoridae from the former, are congruent with the "lyonsiid" and "thraciid" clades found by Dreyer *et al.* (2003) and Harper *et al.* (2006). As explained in section 5.3.2.2 above, absence of Pandoridae from clade F is interpreted as due to multiple secondary losses along the branch leading to this family.

Both clades are characterised by a wide range of morphologies and ecologies which have hitherto prevented the recognition of putative synapomorphies. Apart from the synapomorphies suggested in section 5.2.4.6 following optimisation of characters used in the present cladistic analyses, members of the "lyonsiid" clade have the left valve larger than the right in height, convexity or both dimensions (pholadomyoids and most bivalve outgroups are equivalve), and spermatozoa with elongated nucleus in the few taxa in which this trait has been studied (Kubo, 1977; Kubo & Ishikawa, 1978; Healy *et al.*, 2008). Members of the "thraciid" clade are apomorphically characterised by the list of features given in section 5.2.4.11 and possess the right valve larger and more convex than the left, except in cementing taxa (the sister-group of the clade, Septibranchia, seems to be plesiomorphically equivalve).

Relationships among families comprising the "thraciid" clade are unclear both herein and in the cladograms recovered by Dreyer *et al.* (2003) and Harper *et al.* (2006). Within the "lyonsiid" clade, molecular data suggests Laternulidae as the most basal family, a position which is compatible with the order of appearance of the component families in the fossil record (Fig. 5.5B–C), whereas the most parsimonious distribution of morphological characters implies an early split of the clade into a clavagelloid lineage and a group comprising lyonsiids and laternulids (Fig. 5.5D).

5.3.2.6 Periplomatidae

Perhaps the most surprising result of the present analyses is the disassociation of the families Periplomatidae and Laternulidae, the former clustering with representatives of the "thraciid" clade in the resulting cladograms (Clade K). These two families have been invariably considered sister-groups (e.g. Boss, 1978; Yonge & Morton, 1980; Morton, 1985*a*) and were recovered as such by Harper *et al.* (2000). In Boss' (1978, p. 421)

opinion "laternulids and periplomatids possess certain remarkable synapomorphies: resilium supported by a buttressed chondrophore, umbos uniquely fissured or cracked, lithodesma boomerang-shaped or subtrigonally arched". Harper *et al.* (2006, p. 416) agrees and notes that although "Thus far we have not been able to include any members of the Periplomatidae in our [molecular] analyses... Based on morphological characters, in particular those of the shell, one might fully expect the periplomatids, with their prominent dorsal crack, internal buttress and chondrophores, to be the sister taxon of the Laternulidae... However, given the other discrepancies between morphological and molecular analyses this cannot be assumed".

The conchological features shared by periplomatids and laternulids are indeed remarkable, but not as numerous as implied by Boss' (1978) list. As explained in detail in section 2.4.1 a boomerang-shaped lithodesma, which was interpreted as additional evidence linking these two families by Boss (1978), Yonge & Morton (1980) and subsequent authors (e.g. Morton, 1985*a*), assumes its trigonal shape during ontogeny due to spacial conflict with the chondrophores, which prevent the ossicle from growing in a posterior direction. Shape of the lithodesma is therefore dependent of the presence of F2 and morphology of its support structures and was, for this reason, excluded from the present analyses.

Similarly, a buttress running radially from the umbonal region and linked to the chondrophores is directly related to the umbonal slit and so was excluded from this study. As explained by (Savazzi, 1990) and discussed in section 4.2.4, posterior to the slit the shell is less convex than it is anterior to the slit and the buttress functions in immobilising the valves in this configuration.

Formation of the umbonal slit itself may also be a consequence of the configuration of the ligament and chondrophores, as suggested by Savazzi (1990). However, because a direct link between the two features seems debatable and at least one anomalodesmatan exists which has chondrophores but does not develop the slit (*Trigonothracia jinxingae*, also recovered in clade K), these were retained as separate characters herein.

Sharing of these attributes was outweighed in the present analyses by the numerous putative synapomorphies linking periplomatids to other representatives of clade K (see section 5.2.4.11 and Figure 5.4). Among these, a glandular area on the internal surface of the right mantle lobe seems exclusive of the group, although it is secondarily lost in a few component taxa.

The configuration of the siphons and siphonal area is particularly distinct in the "thraciid" and "lyonsiid" clades. Other than discrete differences recovered as synapomorphies in the present study (e.g. tentacles with apical ciliated sense receptor in the "lyonsiid" clade), the two groups also differ in features showing continuous variation for Anomalodesmata as a whole but well-defined, discrete extremes if comparisons are

restricted to the two clades now under consideration. Members of the "thraciid" clade are characterised by a deep posterior embayment of the mantle margins which shelters long, separate siphons upon withdrawal (siphonal space or embayment). When present, the fourth pallial aperture opens within this embayment. Conversely, within the "lyonsiid" clade a siphonal embayment is lacking so that the fourth pallial aperture opens along the ventral mantle margin instead of posteriorly.

The formation of mucus-lined passages through the sediment is another siphonal character shared between at least a few thraciids and periplomatids, which has not been recorded in any other bivalve group (Yonge, 1937; Morton, 1981*a*; Sartori & Domaneschi, 2005). However, this behavioural character is methodologically difficult to determine and might have a larger taxonomic distribution than currently realised.

Finally, although convergent origins of the umbonal slit in periplomatids and laternulids are difficult to envisage, selective pressure for increased depth of burial may have played a significant role, as discussed in section 4.2.4.

An alternative solution is, of course, to consider that the present analyses failed to recover the true sister-group relationships of periplomatids, as I have argued in the case of pandorids.

In any case, the surprising disassociation of periplomatids and laternulids stimulate further research and highlight the importance of testing their relationships using independent evidence derived from either additional morphological characters (one could investigate, for instance, whether the nucleus of spermatozoa are elongated in periplomatids as they are in laternulids and lyonsiids), or molecular sequences.

5.3.2.7 Septibranchia

In the present study Septibranchia was found monophyletic and closer to clade K than any other anomalodesmatan group. Harper *et al.* (2000, p. 134) had found a sister-group relationship between the group and clavagelloids, in an admittedly "slightly anomalous placement which supports none of the previous hypotheses for their relationships and deserves further investigation". In subsequent molecular studies of the group, most septibranchs were recovered in a basal region of uncertain relationships whereas the euciroid *Euciroa eburnea* and cuspidariid *Myonera* sp. appeared as successive sister-groups to the "thraciid" clade (Dreyer *et al.*, 2003; Harper *et al.*, 2006). Searches with *Myonera* excluded and the remaining septibranchs constrained to be monophyletic found "insignificantly less optimal trees" (Dreyer *et al.*, 2003, p. 242), in which the taxon appears as the sister-group of the "thraciid" clade, i.e., in the same position recovered in the present analyses (Fig. 5.5C).

5.4 Conclusions

Cladistic analyses of the largest morphological dataset compiled to date for anomalodesmatan bivalves yielded cladograms which are in general agreement with the best estimates produced by molecular data alone (Fig. 5.5).

The largest discrepancy between cladograms produced herein to those of Dreyer *et al.* (2003) and Harper *et al.* (2006) concerns the position of Pandoridae, recovered as the most basal anomalodesmatan clade by parsimony analyses of the morphological matrix. Such placement is rendered untenable by the fossil record of the group and interpreted here as due to secondary losses of several key anomalodesmatan anatomical features along the branch leading to the family.

Exempted from the anomalous position of Pandoridae, the present analyses tested and confirmed for the first time in a cladistic context the long-held assertion that Pholadomyoidea comprises the most basal extant anomalodesmatan clade.

Septibranchia was supported as a monophyletic group, a finding that is in agreement to the previous morphological study of Harper *et al.* (2000) and compatible with currently available molecular trees, which neither support nor reject its status as a clade.

Clavagelloidea is also monophyletic, in accordance with most classifications (but see Morton, 2007) and all previous cladistic studies.

Monophyly of a clade joining Periplomatidae and Laternulidae, unanimous in pre-cladistic classifications and supported by Harper *et al.* (2000), is rejected herein and the former family recovered as an additional component of the "thraciid" clade of Dreyer *et al.* (2003; clade K herein).

Incongruences between pre-cladistic classifications and the "total evidence" tree produced by Harper *et al.* (2000) on the one hand, and all subsequent anomalodesmatan cladograms on the other (Dreyer *et al.*, 2003; Harper *et al.*, 2006; this study) concern the interrelationships of thracioid, pandoroid and clavagelloid taxa. These are interpreted as due to limited taxonomic sampling in Harper *et al.*'s (2000) study and a more exhaustive and rigorous character analysis in the present investigation. Enhanced taxonomic sampling not only renders the reconstruction of each clade's bauplan more likely, but also subjects phylogenetic hypotheses to a severer test because each additional taxon with different combinations of character states will necessarily alter the most parsimonious reconstruction of state transitions.

Chapter 6

Anomalodesmatan phylogeny and evolutionary trends

In the previous chapter a new hypothesis for the sister-group relationships within extant anomalodesmatans was presented, which seems broadly congruent with estimates derived from the molecular studies of Dreyer *et al.* (2003) and Harper *et al.* (2006). The clades recovered by the independent datasets analysed herein and by those authors are significantly different from those suggested in classifications of the group or in the less comprehensive cladistic studies of Boss (1978) and Harper *et al.* (2000). This has important implications to our understanding of anomalodesmatan phylogeny.

However, before plunging into a discussion of anomalodesmatan evolution it is important to note that despite the general agreement in the composition of the main clades (equivalent to superfamilies and above), suggested interrelationships within these groups differed between previous molecular and the present morphological hypotheses. For instance, within the "lyonsiid" clade of Dreyer *et al.* (2003, Clade F herein), molecular analyses favoured Laternulidae as the most basal taxon, whereas in the present study an early split between clavagelloids and Clade H (Lyonsiidae + Laternulidae) was recovered (see Fig. 5.5).

Because the species sampled from each supraspecific taxon in existing matrices are different and the monophyly of several genera and families is unsupported or rejected by the cladograms, it is not possible at present to solve these conflicts by performing combined analyses of morphological and molecular datasets.

Fortunately, the anomalodesmatan fossil record appears complete enough to be useful in discriminating between cladistic hypotheses (Harper *et al.*, 2000) and it is therefore reasonable to choose, among competing topologies, the one which assumes the fewest and shortest stratigraphic gaps.

Using the above criterion, this final chapter moves from competing cladograms to

a tentative phylogeny of Anomalodesmata, proposed here as a compromise between morphological and molecular hypotheses of relationship among Recent taxa calibrated against their known stratigraphic ranges. In the light of this phylogeny, evolutionary trends suggested by previous authors are discussed and a novel interpretation of the Cenozoic radiation of Anomalodesmata presented.

6.1 Fossil record

The present volume is concerned with the morphology and phylogenetic relationships of Recent anomalodesmatans. Nevertheless, because patterns recognised in the fossil record have deeply influenced views of anomalodesmatan evolution, and some conclusions from the present study have implications to established hypotheses of ancestor-descendant relationships, extinct families currently purported to belong in the group are briefly considered below. However, these fossil taxa were deliberately not incorporated to the phylogeny presented in Figure 6.3. After all, most of these extinct groups are in much need of reassessment and, having undertaken only cursory observations of fossil material, I shall limit this discussion to a critical review of ideas concerning their possible relationships to later anomalodesmatans, particularly to members of the crown group.

The fossil record of anomalodesmatans extends back to the Ordovician period and has been the subject of numerous accounts, including comprehensive reviews by Runnegar (1974) and Morris *et al.* (1991).

As noted by Morris *et al.* (1991) and Harper *et al.* (2006), anomalodesmatans are rather common and diverse in the Middle and Late Palaeozoic and Mesozoic, but become less prominent subsequently. Figure 6.1 plots changing generic diversity of each family currently purported to belong in the clade with a known fossil record.

6.1.1 Ucumariidae and other Early Ordovician taxa

Sánchez (in Sánchez & Vaccari, 2003) erected the family Ucumariidae for an edentulous Early Ordovician (Late Tremadocian) bivalve which she considered to represent, mostly on the basis of its pustulose ornamentation, the earliest known representative of the Anomalodesmata.

She also suggested that *Arenigomya carinata*, another Early Ordovician (Lower Arenig) bivalve, described by Cope (1996*b*) as a member of the anomalodesmatan family Grammysiidae, could be included in Ucumariidae because it shares with *Ucumaris conradoi* a granulose texture and conspicuous radial sculpture covering the entire body of the shell (Fig. 6.2A). In a series of subsequent papers, Sánchez (2005, 2006, 2008) erected two other Early Ordovician bivalve families (Lipanellidae and Goniophorinidae)

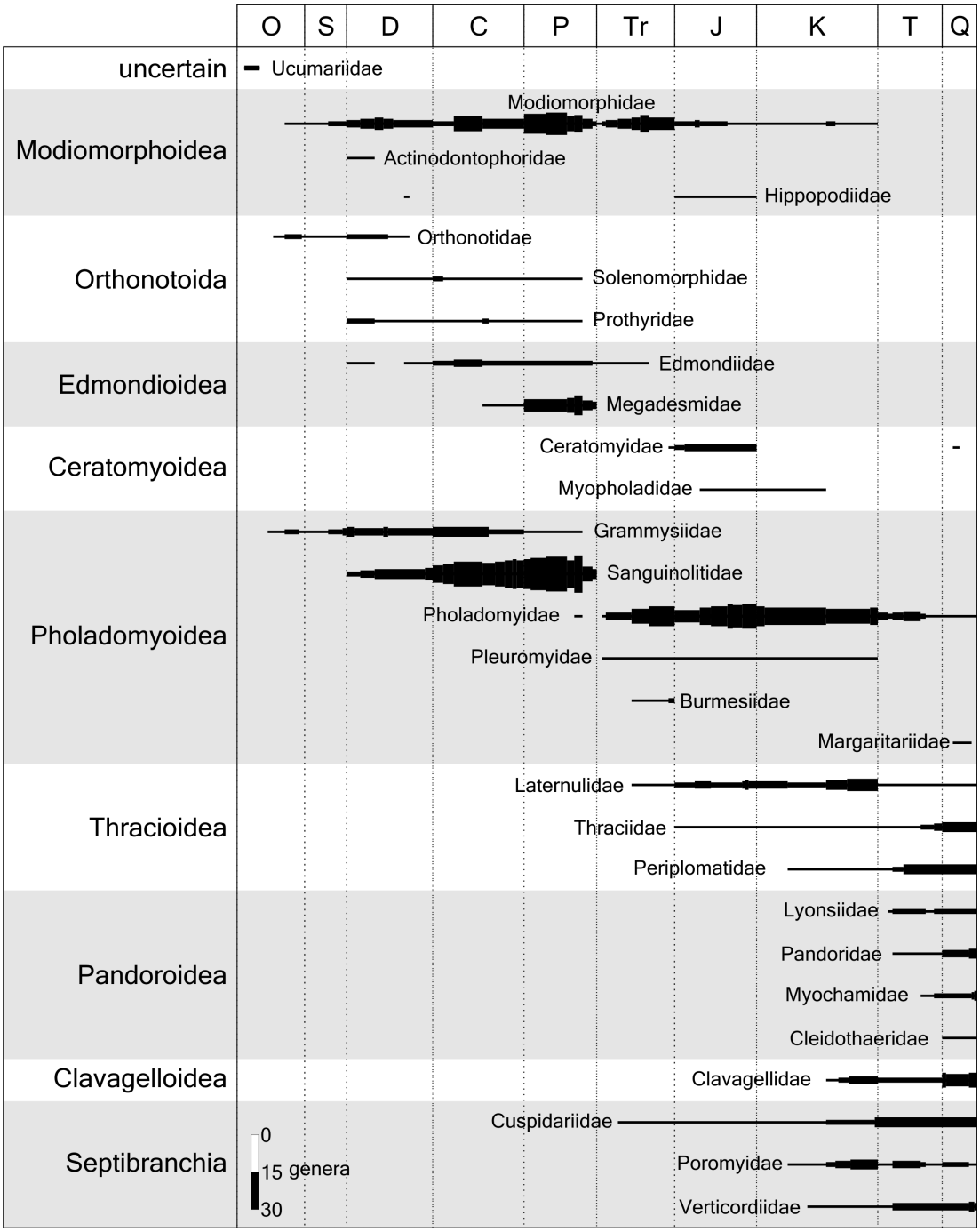


Figure 6.1: Changing patterns of global generic diversity in each anomalodesmatan family over the course of the Phanerozoic. Stratigraphic range data obtained from Sepkoski's (2002) compendium, which does not include all genera comprising the listed families, nor taxa represented solely by extant material. No effort was made to complement or correct the database, except for the addition of Ucumariidae. Assignment of individual genera to familial and suprafamilial taxa followed the classificatory schemes of Sánchez & Vaccari (2003) for Ucumariidae, Fang & Morris (1997) for Modiomorphoidea, Morris *et al.* (1991) for Orthonotoida, Edmondioidea and Pholadomyoidea (part), Runnegar (1974) for Ceratomyoidea and Pholadomyoidea (part), and Newell *et al.* (1969*a*) for the remaining taxa.

and put forward the hypothesis that these forms "integrate a major group of edentulous bivalves, a lineage of which — the ucumariids — probably gave rise to Anomalodesmata" (Sánchez, 2006, p. 113).

Sánchez's hypothesis is in line with earlier suggestions that the origin of the Anomalodesmata should be sought among modioliform bivalves (Pojeta & Runnegar, 1985; Cope, 1997) and I have no objection to the tentative inclusion of these families in the clade. After all, ucumariids display calcified periostracal sculpture in the form of granules or spikes, an attribute that has long been considered a synapomorphy of Anomalodesmata (e.g. by Runnegar, 1974; Morris *et al.*, 1991), and which was recovered as such in the present analyses (after dismissal of the basal position of Pandoridae).

However, ucumariids display features which, if not artefacts of preservation, are derived and unlikely to have characterised the common ancestor of anomalodesmatans. The most important of these features is the apparent absence of ligament nymphs in these taxa. Cope (1996*b*) confidently described the hinge of *Arenigomya* as comprising two spoon-shaped subumbonal structures which could have housed an internal ligament, and Sánchez (in Sánchez & Vaccari, 2003, p. 419) argued that absence of nymphal ridges in *Ucumaris* "could be interpreted as evidence that nymphs developed later" within Anomalodesmata. Notwithstanding, the studies of Waller (1990, 1998) have shown that an external ligament supported by nymphs (parivincular) is a synapomorphy of Heteroconchia, primitively present in the anomalodesmatan clade, a result which has been unanimously corroborated by recent cladistic analyses of bivalves based on molecular and combined data (Giribet & Wheeler, 2002; Giribet & Distel, 2003; Taylor *et al.*, 2007). Significantly, these structures are present in most undoubted Palaeozoic anomalodesmatans whose hinge morphology is known (Runnegar, 1974; Morris *et al.*, 1991).

Hence, the lineage recognised by Sánchez (2006) may represent an early offshoot of the main anomalodesmatan branch, apomorphically characterised by an internal ligament, but it seems unlikely that ucumariids are ancestors of later anomalodesmatans.

6.1.2 Modiomorphoidea

Until recently, Modiomorphoidea had been the repository of most Palaeozoic modioliform bivalves, ranging from Early Ordovician to Late Permian, and commonly considered related to or the direct ancestors of extant mussels (e.g. by Soot-Ryen, 1955; Cox, 1960; Pojeta, 1971, 1978; Pojeta & Runnegar, 1985; Carter, 1990). However, as noted by Pojeta (1971), the *Treatise* concept of the superfamily (LaRocque & Newell, 1969) was overly broad and the group seemed to contain a number of unrelated lineages. Since then, the superfamily has been deflated by the erection of several higher taxa for

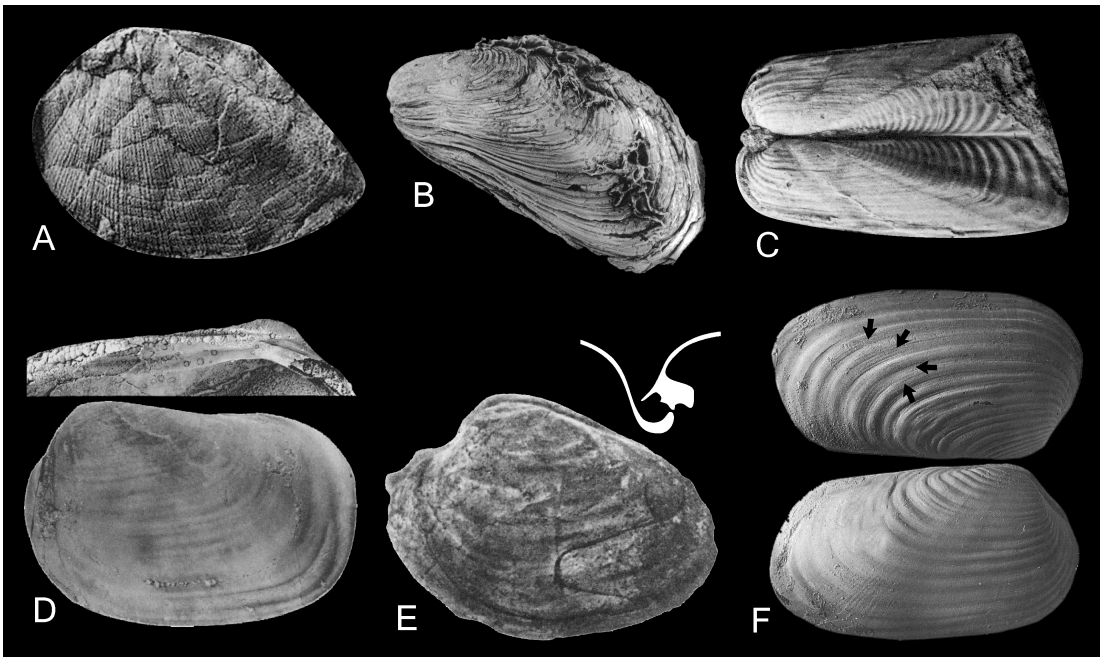


Figure 6.2: Representatives of each major extinct anomalodesmatan taxon, showing part of the broad range of morphologies exhibited by the group. **A**. Ucumariid *Arenigomya carinata*, after Cope (1996*a*, pl. 7, fig. 12). **B**. Modiomorphid *Modiomorpha concentrica*, after Bailey (1983, fig. 46a). **C**. Orthonotid *Orthonota undulata*, after Pojeta *et al.* (1986, pl. 19, fig. 2). **D**. Internal mold of the edmondiid *Edmondia oblonga* (bottom) and silicified hinge of *Edmondia* sp. showing the lamellar plate (top), after Runnegar & Newell (1974, figs 4 and 2a, respectively). **E**. Internal mold of the ceratomyoid *Gresslya peregrina* (bottom) after Cox (1969*a*, fig. F18, 2a), and schematic transverse section through the hinge of *Ceratomya bajociana* (top), after Cox (1963, fig. 2b). **F**. Sanguinolitid *Wilkingia regularis*, with position of pallial sinus indicated by arrows on the left side of the internal mold (top), after Morris *et al.* (1991, fig. 22a,b).

forms previously placed in the superfamily, and by transfer of a number of individual genera elsewhere (see Fang & Morris, 1997, for a review).

Bailey (1983) analysed well-preserved material of the type species of the superfamily (*Modiomorpha concentrica*, Fig. 6.2B) and recorded ligamental nymphs, a single cardinal tooth in the left valve and weak lateral teeth, characters which suggested heteroconch affinities rather than the more usual placement among pteriomorphians. Although Pojeta (1986) challenged the interpretation of a parivincular ligament and lateral teeth in the species, Carter (1990) confirmed both of Bailey's observations and figured transverse sections through the hinge of the species which unambiguously revealed dorsally projecting nymphal ridges. Based on the presence of nymphs, simple dentition, wholly aragonitic shell microstructure and details of the sculpture of the early dissoconch, Waller (1990) favoured the inclusion of Modiomorphidae in Anomalodesmata, a suggestion which was followed by Johnston (1993).

Notwithstanding, noting that not all genera traditionally placed in Modiomorphoidea possess a parivincular ligament, Fang & Morris (1997) restricted the scope of the superfamily, which they also placed in Anomalodesmata, to taxa bearing nymphs. All genera without these support structures were assigned by Fang & Morris (1997) to another lineage, the Modiolopsoidea (families Modiolopsidae, Colpomyidae, and Modiolodontidae), thought to be related to mytilids. Additionally, Fang & Morris (1997) removed the families Actinodontophoridae and Hippopodiidae from Unionoidea and Crassateloidea, respectively, and assigned them to Modiomorphoidea. The former family was placed in the group due to the overall similarity in shell shape and ligament character between its components and Modiomorphidae, despite the presence of numerous, elongate hinge teeth radiating from the beaks of actinodontophorids. The latter was included in Modiomorphoidea because of "the similar overall form and similarity of the known musculature" (Fang & Morris, 1997, p. 56).

Carter & Tevesz (1978) and more recently Schneider & Carter (2001) revealed the presence of aragonitic spikes of probable periostracal origin on the shell exterior of *M. concentrica*, a character which endorses placement of the species within Anomalodesmata. If modiomorphids are indeed anomalodesmatans, as the currently available evidence seems to indicate, then they represent an early radiation of the group into epibyssate habits, a mode of life which is only known to occur within undoubted anomalodesmatans in a few extant lyonsiids (Prezant, 1981*a*) and poromyids (Leal, 2008).

This derived mode of life with its attendant morphological adaptations, namely retention of a functional byssal apparatus into adulthood and pronounced heteromyarian form, precludes assignment of modiomorphids as putative ancestors of Mesozoic and Cenozoic anomalodesmatan clades, all of which retain an approximately isomyarian shape and appear to have descended from burrowing forms. Although one Cenozoic anomalodesmatan genus is known which is markedly heteromyarian (*Mytilimeria*), it bears an internal ligament and circular shell shape (Yonge, 1952; Prezant, 1981*a*), features that make derivation from modiomorphids rather unlikely.

6.1.3 Orthonotoida

This is a problematic ensemble of elongate, burrowing bivalves, with a soleniform shell, external, opisthodetic ligament and a posterior gape (Fig. 6.2C). Hinge and internal characters are poorly known and no representative has yet been found which display pustulose ornamentation.

Orthonotidae was referred to Edmondioidea by Newell (1965), and later to Pholadomyoidea by Newell *et al.* (1969*a*). However, it was removed from the Anomalodesmata by subsequent authors, who stressed the similarity of the group with the

living Solenoidea (e.g. Pojeta, 1971; Pojeta & Runnegar, 1985; Pojeta, 1986; Pojeta & Gilbert-Tomlinson, 1977; Runnegar, 1974).

Morris *et al.* (1991) transferred a number of elongated genera previously treated under the anomalodesmatan family Grammysiidae to Solenomorphidae and doubtfully suggested affinities between this group and Orthonotidae, grouping both taxa under a order of their own (Orthonotoida). Morris *et al.* (1991) dismissed a relationship of the order with Solenoidea for considering that a soleniform shape has arisen convergently at least four times in bivalves and, commenting on a series of species of *Solenomorpha* which grade into what appear to be the earliest representatives of the family Cuspidariidae, tentatively returned Orthonotoida to Anomalodesmata.

Placement of Orthonotoida in Anomalodesmata is therefore largely based on a possible relationship between *Solenomorpha* and Cuspidariidae, which is a problematic criterion because: (1) there is evidence of taxonomic confusion involving the first alleged cuspidariids; and (2) considering solenomorphids as stem-group cuspidariids in the light of the sister-group relationships suggested by the present cladistic study implies that splits between the major anomalodesmatan clades had occurred by the Devonian, with long stratigraphic gaps characterising the fossil record of most groups.

Regarding the first point, although muscle scars left by the septal muscles may be used as an aid to the unequivocal identification of fossil cuspidariids (Runnegar, 1974), Triassic and Jurassic forms referred to the family have been identified on the basis of gross external morphology alone. Harper *et al.* (2002) provided an interesting example of the perils of this practice by investigating one of the oldest alleged members of the family, whose association with brackish-water facies had raised doubts over its true identity. By conducting detailed investigations of shell microstructure and musculature, Harper *et al.* (2002) revealed that the species in question is better regarded as a member of the myoid family Corbulidae, despite its remarkable resemblance to cuspidariids. Those authors identified two Late Cretaceous (Maastrichtian) species with clear septal muscle scars as the earliest unequivocal cuspidariids and concluded that the fossil record of the family has been erroneously extended by the inclusion of dubious taxa.

As Morris *et al.* (1991, p. 52) themselves remark, Orthonotoida is tentatively retained in Anomalodesmata largely because they "are better placed there than elsewhere" but until well-preserved hinges are described for representatives of the group, their systematic position remains debatable.

6.1.4 Edmondioidea

Edmondioids are shallow burrowers displaying short, robust shells, with closed valve margins or only a narrow siphonal gape (Fig. 6.2D). The ligament is arguably pariv-

incular (but see section 2.4.2) and a pallial sinus is either lacking or represented only by a slight indentation of the pallial line. Of the two component families, edmondiids are found chiefly in strata laid down in temperate and warm seas, now in the northern hemisphere, whereas megadesmids mainly occur in the cold and cold-temperate waters of the southern hemisphere of Permian times (Runnegar & Newell, 1971, 1974; Morris *et al.*, 1991). Of all Palaeozoic anomalodesmatan families, Megadesmidae is without doubt the most extensively studied, with several monographs published on its representatives (Newell, 1956; Waterhouse, 1965, 1966, 1969*b*; Runnegar, 1965, 1966, 1967; Runnegar & Newell, 1971), as well as a cladistic analysis including 14 component genera (Simões *et al.*, 1997).

Influenced by the work of Runnegar and colleagues (Runnegar, 1965, 1966, 1967, 1968, 1974; Runnegar & Newell, 1974), most workers place the two component families within the superfamily Pholadomyoidea. However, Morris *et al.* (1991) emphasised the difficulties in finding reliable synapomorphies linking edmondiids and megadesmids to mainstream anomalodesmatans, and commented that these families are placed in the group largely by tradition. Based on the rare occurrence of calcified periostracal elements in representatives of both families, Morris *et al.* (1991) supported their inclusion in Anomalodesmata, but advocated their allocation to a separate superfamily, defined by the presence of a hinge plate reinforced internally by a ridge projecting into the shell cavity (lamellar or internal plate of authors). Morris *et al.* (1991) also restricted the concept of Megadesmidae considerably from that of Runnegar (1974) by transferring *Myonia* and the deeper-burrowing genera *Vacunella* and *Australomya* to Sanguinolitidae.

Other than the lamellar plate, which sets edmondioids apart from the lineage leading to crown-group Anomalodesmata, Simões *et al.* (1997) identified as a synapomorphy of Megadesmidae a S-shaped tooth derived from a fold in the cardinal margin of the left valve which has been historically adopted as a distinguishing feature of the family (e.g. Newell, 1956; Runnegar, 1974).

6.1.5 Ceratomyoidea

This exclusively Mesozoic group includes shallow and deep-burrowing, inequivalve forms (Fig. 6.2E) with overlapping dorsal shell margins and an assymetrical, subinternal ligament which is supported by a nymph in the left valve but connected to the internal surface of the right valve (Cox, 1963). Radiating rows of minute granules, probably of periostracal origin, are known in at least some representatives (Runnegar, 1965).

Ceratomyidae and Myopholadidae, the two component families, figured among pholadomyoids in the *Treatise* (Cox, 1969*a*,*b*) but Runnegar (1974), who attributed great

importance to the configuration of the hinge ligament in his classificatory scheme, erected the superfamily Ceratomyoidea to reflect the unique structure of the organ in the group.

Recognising some degree of overlap between the dorsal valve margins of the genus *Megadesmus* and a number of other similarities with *Ceratomya*, including overall shape, ornament and musculature, Runnegar (1965) suggested that ceratomyoids could be directly derived from edmondioids. Morris *et al.* (1991) also noted similarities in size, shape and sculpture between the edmondiid genus *Cardiomorpha* and *Ceratomya*, but preferred to regard these as consequences of convergent evolution for deeming the shell form of the oldest ceratomyid genus (*Pteromya*) significantly distinct.

As discussed in chapter 2, Runnegar (1974) envisaged the evolution of anomalodesmatan ligament grades as a gradual process of ventral migration of the organ. Hence, he interpreted ceratomyoids, with their subinternal ligaments, as intermediate between edmondioids and pandoroids, and the only known shallow burrowing Mesozoic anomalodesmatans from which representatives of the latter superfamily could have evolved (see footnote in Yonge & Morton, 1980, p. 286).

However, the model proposed in section 2.5 on the basis of detailed observations of the morphology and development of the ligament of extant anomalodesmatans derives the pandoroid adult ligament from paedomorphic retention of the early juvenile fibrous layer, which is primitively internal in anomalodesmatans.

Hence, rather than representing an intermediate condition between external and internal ligaments, the asymmetrical, subinternal ligament of ceratomyoids is presumably a synapomorphy of the group which, as suggested by Yonge & Morton (1980, p. 286), represents an "evolutionary dead end". Ceratomyoidea should no longer be considered to include the ancestors of anomalodesmatans with internal ligaments.

6.1.6 Pholadomyoidea

Historically, the superfamily Pholadomyoidea has been the repository of all extinct anomalodesmatan genera bearing an external, parivincular ligament (e.g. Runnegar, 1974) and it is therefore unsurprising that its concept has become very broad (Morris *et al.*, 1991).

The earliest undoubted anomalodesmatans, the Middle Ordovician genera *Cuneamya* and *Rhytimya* (Pojeta, 1978), are traditionally placed in Grammysiidae, a family characterised by oval to elongated shells without a pallial sinus, and commonly displaying one or a few radial furrows (sulci) running from the umbones to the ventral valve margins. Grammysiids are prominent members of many shallow water Palaeozoic faunas,

living either shallowly burrowed in soft substrata or fixed by byssal threads in infaunal and semi-infaunal positions (Bambach, 1971; Marsh, 1984; Rehfeld & Mehl, 1989).

Morris *et al.* (1991) regarded Grammysiidae as a paraphyletic taxon which includes the stem group of Sanguinolitidae. According to these authors the latter family, diagnosed by elongate shells with a lunule and a flattish escutcheon, differs essentially from grammysiids in the development of deeper-burrowing, siphonate forms (e.g. *Undulomya*, *Wilkingia*, Fig. 6.2F) that may have given rise to Pholadomyidae. Runnegar (1974) also argued for an evolutionary lineage linking elongate, shallow-burrowing grammysiid genera such as *Cuneamya* to deep-burrowing *Wilkingia* and subsequently to Upper Triassic to Recent *Pholadomya*. However, neither Runnegar (1974) nor earlier reviewers of the group (e.g. Newell, 1956; Newell *et al.*, 1969*a*; Dickins, 1963; Waterhouse, 1965) made use of Sanguinolitidae in their classificatory schemes but split sanguinolitid genera among grammysiids, pholadomyids and megadesmids. Despite the contrasts in concept and boundaries between these families applied by different authors, at times rather significant, all implied that they are closely related.

There seems to be general agreement among palaeontologists that the family Sanguinolitidae sensu Morris *et al.* (1991) has evolved from a species classed under Grammysiidae and includes the ancestor of crown-group Anomalodesmata. Hence, both families are paraphyletic as currently construed but features such as radial sulci may allow the recognition of monophyletic sub-groups within these groups in future studies.

Apart from the taxa above, three small post-Palaeozoic families have been commonly included in Pholadomyoidea.

The cosmopolitan, Triassic to Cretaceous genus *Pleuromya* is deep-burrowing and similar in overall shape to some sanguinolitid and pholadomyid genera. However, it is generally placed in a family of its own for bearing short, slightly hollowed projections of the dorsal valve margins below and slightly anterior to the beak, which overlap one another and might have supported a small, internal ligament (Dall, 1913; Cox, 1969*c*). Although these overlapping projections might have been similar to the ligament support structures of ceratomyoids, *Pleuromya* has an external ligament supported by nymphs and is for this reason normally referred to the Pholadomyoidea instead. Considering current knowledge of the presence of internal and external resilient components in the ligament of numerous extant anomalodesmatans, including *Pholadomya candida* and parilimyids (see chapter 2), re-examination of these Mesozoic shells could be valuable. However, judging from the photographs and interpretative diagrams by Cox (1969*c*), the overlapping protuberances of left and right valves differ from hinge structures found in other anomalodesmatans and may be considered apomorphic features of pleuromyids.

Burmesiidae is a poorly studied family restricted to the Upper Triassic of Asia which comprises two elongated genera with an elaborate ornamentation of radial ridges

and commarginal folds, the ridges predominating on the middle of each valve, as well as rows of minute granules (Healey, 1908). The hinge is edentulous but bears an internal ligament supported by large chondrophores. In his description of the family, Healey (1908) regarded burmesiids as intermediate between pholadomyids and laternulids, highlighting the similarity in ornamentation to members of the former family and in hinge structure to those of the latter. Curiously, Runnegar (1974) made no mention of burmesiids in his comprehensive review of Anomalodesmata.

Margaritariidae is the only Cenozoic anomalodesmatan family without living representatives. It comprises a single genus, distributed in Middle and Upper Miocene deposits from southern Maryland to South Caroline, U.S.A., and also known from the Upper Eocene of Louisiana (Vokes, 1964). Although *Margaritaria* displays only a shallow pallial sinus, Vokes (1964) interpreted the genus as deep-burrowing on the basis of its narrow anterior and wide posterior gapes and referred it to Pholadomyoidea for bearing an inner nacreous shell microstructure, gapes, radial ribs along only part of the flank and a parivincular ligament. In the *Treatise*, Keen (1969*c*) transferred Margaritariidae to Pandoroidea, but Runnegar (1974) subsequently returned it to Pholadomyoidea.

Although the extant representatives of Pholadomyoidea were recovered in a monophyletic group both here and in the previous cladistic study by Harper *et al.* (2000), it is evident that the superfamily is also a group of convenience because the alternative view would indicate that clade E has been separate from monophyletic Pholadomyoidea at least since the Middle Ordovician. Significantly, all features listed in diagnoses of the superfamily are plesiomorphic for Anomalodesmata or for even more inclusive bivalve groups (e.g. external ligament; burrowing habit).

6.1.7 Extant families

Apart from Spheniopsidae, whose status as an anomalodesmatan clade requires confirmation, the only extant families not represented in Figure 6.1 are Parilimyidae, Lyonsiellidae and Euciroidae. This is mostly a taxonomic artefact because the classification of Newell *et al.* (1969*b*), followed herein for the assignment of extant genera listed in Sepkoski's (2002) database, did not include these families.

Parilimyidae was erected by Morton (1982) for three extant genera, *Parilimya*, *Panacca* and *Nipponopanacca*, among which *Panacca* was regarded by Runnegar (1974) as closely related to the Jurassic (Callovian) *Procardia*. Scarlato & Starobogatov (1983, translated by Poutiers & Bernard, 1995, appendix 2) subsequently referred not only the latter genus, but also the Jurassic (Toarcian) *Bucardiomya* to the family. Hence, derivation of Parilimyidae, presumably as an offshoot of paraphyletic Pholadomyidae, may have occurred as early as the Early Jurassic. Unfortunately, internal features of

the suspected Jurassic parilimyids are currently unknown, so that presence of a separate muscle scar for hypertrophied siphonal retractors (the only conchological synapomorphy of the family recovered in the present study) remains conjectural.

Lyonsiellidae and Euciroidae have only recently been adopted in most classificatory schemes, comprising genera previously referred to Verticordiidae. Sepkoski's (2002) database lists only one extant genus, *Laevicordia*, which is now commonly referred to Lyonsiellidae. It first appears in the Pliocene (Keen, 1969*a*). Although euciroids are not listed, it seems likely that subsequent revision of Verticordiidae might result in the transferral of fossil genera not only to Euciroidae but also to Lyonsiellidae.

6.2 Tentative phylogeny of extant anomalodesmatans

Figure 6.3 represents a tentative phylogeny of extant anomalodesmatan families, combining the summary morphological cladogram presented herein (Fig. 5.5D) with Harper *et al.*'s (2006) preferred hypothesis of relationships (Fig. 5.5C; constrained for monophyletic Septibranchia). Conflicts were resolved, when possible, by the stratigraphic order of appearance of taxa. The fossil record of Cuspidariidae has been considered to extend back to the Late Cretaceous rather than Triassic due to the taxonomic problems noted by Harper *et al.* (2002) and briefly discussed in section 6.1.3.

Because most traditional anomalodesmatan families are probably merophyletic and for reasons which will become clear when evolutionary trends are discussed, I have favoured derivation of clades from ancestors classed within a nominal family (offshoots) over early splits between lineages. The latter alternative would imply lineages have an abbreviated fossil records with most of their initial history missing.

Extant pholadomyoids are considered the most basal clade of the crown group, in accordance not only with the morphological cladograms presented herein and by Harper *et al.* (2000), but also with the longevity of Pholadomyidae. Accepting referral of *Procardia* and related genera to Parilimyidae, a split between this family and Pholadomyidae is thought to have happened by the Middle Jurassic.

Among representatives of the "lyonsiid" clade, Laternulidae is the first family to appear in the fossil record and was therefore considered to contain the ancestors of the remaining familial groups. The basal position of Laternulidae depicted in Figure 6.3 favours the topology suggested by molecular cladograms (Dreyer *et al.*, 2003; Harper *et al.*, 2006) over that recovered in the present analyses.

Relationships within septibranchs are currently unclear. Because most representatives of the clade live in deep sea habitats with low preservation potential, they may have split from the "thraciid" clade considerably earlier than the first recognised fossil

poromyids, as indicated in Figure 6.3, or they may represent an offshoot from Mesozoic representatives of the polyphyletic family Thraciidae.

Within the "thraciid" clade, Periplomatidae is envisaged as an offshoot from the main lineage of thraciids, which evolved into deeper burrowing modes of life with attendant changes in ligament morphology and pallial musculature. The Cenozoic families Cleidothaeridae and Myochamidae were also considered derived from ancestors classed within Thraciidae, a hypothesis which seems compatible with both previous molecular and present morphological cladograms.

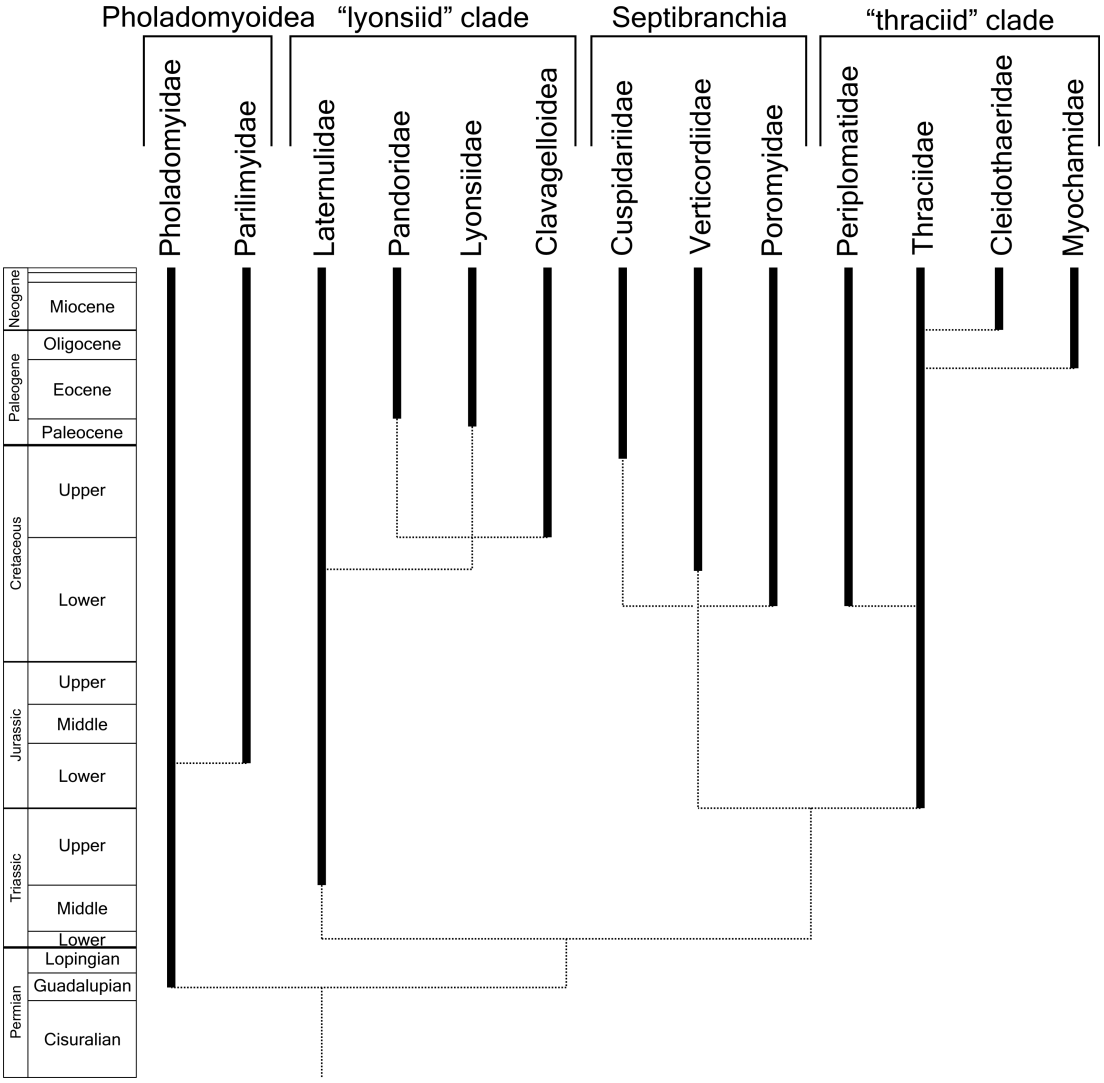


Figure 6.3: Phylogeny of extant anomalodesmatans. Stratigraphic ranges are represented by solid vertical lines and suggested relationships indicated by horizontal dotted lines.

6.3 Evolutionary trends

While most palaeontologists have restricted their treatments of the anomalodesmatan fossil record to the systematics of families and sub-groups, often attempting to recognise ancestor-descendant relationships (e.g. Waterhouse, 1966), Runnegar (1974) also identified patterns which have deeply influenced views of anomalodesmatan evolution. These trends are discussed below in the light of present findings.

6.3.1 Ventral migration of the ligament

The first trend identified by Runnegar (1974) is towards the ventral migration of the ligament with decreasing geological age. This pattern, discussed in section 2.5, forms the basis of the postulated derivation of Pandoroidea sensu Newell *et al.* (1969*b*) (and including Verticordiidae) from pholadomyoids via a ceratomyoid intermediate form (see Runnegar, 1974, text-fig. 3).

Curiously, although Runnegar (1974) and subsequent authors (e.g. Yonge & Morton, 1980; Morton, 1981*b*, 1985*a*) have regarded this trend as the most important in the establishment of anomalodesmatan phylogenetic relationships, a process to account for the shift in the position of the ligament has never been postulated. In other words, the question of what selective pressure could have led to internalisation of the organ has remained unaddressed.

Following a critical review of ligament structure in Anomalodesmata I have suggested that the idea of ventral migration of the organ be restricted to shifts in the position of the secondly formed fibrous ligament layer (F2) as an adaptation for deep-burrowing. The pandoroid (also termed simple sunken or lyonsiid) ligament comprises solely the first formed fibrous layer (F1) and is better regarded as paedomorphic. This new hypothesis is explained in detail in chapter 2.

6.3.2 Adaptations for deep-burrowing

Runnegar (1974) conceived the evolution of deep-burrowing anomalodesmatans as an irreversible process which occurred iteratively from shallow-burrowing ancestors. In his words: "I envisage a slowly evolving stock of shallow burrowing species which may periodically and relatively rapidly produce deeper burrowing forms. This process is assumed to be irreversible, that is, shells adapted for deep burrowing are more specialised and are unlikely to produce descendents which lack these adaptations" (Runnegar, 1974, p. 910).

Although Runnegar (1974) presents convincing evidence of this trend in Megadesmidae, Sanguinolitidae and other ancient anomalodesmatan lineages, the phylogeny de-

vised herein for extant taxa contradicts the pattern, suggesting it is not a valid explanation for the Cretaceous and Cenozoic radiations of anomalodesmatans. Derivations of pandorids, lyonsiids and clavagelloids from laternulids, and of myochamids and cleidothaerids from thraciids, as suggested in Figure 6.3, challenge this trend because laternulids and thraciids burrow deeper than the remaining listed representatives of Clades F and K, respectively.

With a transition from shallow-burrowing ceratomyoids to pandoroids refuted on the basis of ligament structure — the asymmetrical ligament of the former taxon is unlikely to have evolved into the plesiomorphically symmetrical "simple sunken" ligament — derivation of the pandoroid families from extinct shallow burrowers would imply long stratigraphic gaps linking the group to sanguinolitids, edmondioids or other Palaeozoic lineages.

Instead, heterochronic changes explain transitions which are opposite to the pattern originally suggested by Runnegar (1974), without assuming long gaps in the fossil record. That is, the radiation of the group into shallow-burrowing and epifaunal modes of life proceeded iteratively from two lineages of deep-burrowers which had split by the beginning of the Jurassic. Evidence for this hypothesis comes mainly from the stratigraphic range of families in Clades F and K, and consideration of the evolution of their morphological traits, as discussed below.

6.3.3 Heterochronic evolution

6.3.3.1 Clavagelloids, pandorids and lyonsiids as offshoots of Laternulidae

The phylogeny drawn in Figure 6.3 implies that clavagelloids, lyonsiids and pandorids form a monophyletic group which evolved from an ancestral species classed within Laternulidae. This renders the latter family paraphyletic, which is at odds with both molecular and morphological cladograms.

In the present study, for example, Laternulidae was recovered with the highest values of the Bremer's index among recovered clades, and supported by synapomorphies which include complex eyes, unique among Anomalodesmata, chondrophores and an umbonal slit. However, cladistic analyses and morphological surveys have so far failed to include any laternulid genus other than *Laternula* and hence the conclusion that complex eyes and other anatomical features are synapomorphies of the family rather than of less inclusive taxonomic units is unwarranted.

And as for the chondrophores supporting F2 and the umbonal slit, which are present in all extant and fossil laternulid genera, both arise concomitantly and relatively late in the ontogeny of *Laternula* (see chapter 2). Hence, a paedomorphic origin of clavagelloids, lyonsiids and pandorids from a laternulid ancestor would explain not only the

structure of the ligament, comprising only F1, but also the absence of a umbonal slit in the latter three families. In fact, although a single heterochronic event of this kind was indicated in Figure 6.3, the possibility of two or more independent events cannot be discarded at present, since features linking clavagelloids, lyonsiids and pandorids which are not displayed by juvenile laternulids were not found in the present investigation.

In addition to these conchological characters, negative allometry of the foot was recognised by Morton (1976) for *Laternula anserifera* and, during the course of this investigation, I have observed in *L. elliptica* not only the same trend in the development of the foot, but also marked positive allometry of the siphons. Hence, juvenile specimens of *L. elliptica* bear short siphons and a long foot which actively secrete byssal threads, being in both aspects similar to shallow-burrowing and endobyssate species placed in Lyonsiidae and Pandoridae.

6.3.3.2 Cleidothaerids and myochamids as offshoots of Thraciidae

Paedomorphosis may similarly explain the derivation of cementing and shallow-burrowing cleidothaerids and myochamids from deep-burrowing ancestors classed in either Thraciidae or Periplomatidae. The first of these possibilities was favoured herein because clade N, recovered in the present morphological cladograms, joins representatives of Thraciidae and Myochamidae but does not include periplomatids.

Because monophyly of a group joining cleidothaerids and myochamids was rejected by both molecular and morphological cladistic analyses of extant anomalodesmatans, derivation of these families was plotted as two independent events in Figure 6.3. Significantly, Boss (1978, p. 422) noted that "The myochamid-cleidothaerid lineage has few known synapomorphies, but the subtrigonally shaped young individuals suggest a close relationship between these rare groups". This last similarity, which was used by Odhner (1917) to refute a possible relationship of *Cleidothaerus pliciferus* to representatives of *Pseudochama*, is also shared by thraciids and periplomatids.

6.3.3.3 Processes

Most evidence is at present circumstantial but it seems likely that different heterochronic processes were involved in the evolution of these lineages. Despite their juvenilised morphology in terms of ligament, foot and siphonal structure, some of the extant epifaunal anomalodesmatan taxa are distinctively larger than their deep-burrowing counterparts (e.g. the epibyssate lyonsiid *Entodesma navicula* and most clavagelloids are larger than laternulids; Yonge, 1952; Morton, 2007). Yet, this does not preclude a transition between the two adaptive zones being achieved by animals of small body size. As explained by Stanley (1972), when body dimensions approach sediment grain size,

the discontinuity between endobyssate and epifaunal modes of life disappears because attaching to a single particle becomes equivalent to attaching to hard substrata.

Thus, the transition from infaunal to epifaunal realms within both the "lyonsiid" and "thraciid" clades is likely to have involved bivalves with paedomorphic anatomy and small body sizes. Both progenesis (earlier sexual maturation) and neoteny (slower rate of development) may produce such combination, but the former process seems more commonly associated with diminished dimensions and may be triggered by selection towards population increase in unpredictable or ephemeral environments (e.g. favouring r-strategists; see Gould, 1977; McKinney & McNamara, 1991, for reviews). Following the invasion of the new ecological niche, an increase in body size marked the evolution of these epifaunal stocks, probably involving hypermorphosis (later maturation and offset of somatic growth).

Hence, the Cenozoic radiation of the Anomalodesmata, often seen as the most remarkable event in the evolutionary history of the group (Morton, 1985*a*; Harper *et al.*, 2000, 2006), has been brought about, it is claimed here, by iterative heterochronic changes affecting at least two lineages of deep-burrowers. Shallow-burrowing and epifaunal descendants of these separate lineages share a simple sunken ligament which is identical to the early juvenile resilium of their putative ancestors. They have been, for this reason, traditionally classed together in an artificial group (Pandoroidea sensu Boss).

Conclusions

In summary, the main hypotheses and conclusions of the present work are:

1. Contrary to the prevailing opinion, ligament structure does not provide an unequivocal guide to anomalodesmatan phylogenetic relationships.

   The plesiomorphic mode of development of the organ in the group is discontinuous, meaning that (at least) two fibrous layers are formed during ontogeny: one in preparation to or soon after metamorphosis (F1), and the other in the early juvenile (F2).

   From this condition, numerous ligament grades were generated within the clade by combinations of three basic and interconnected processes: calcification of the sagittal sector of F1 into a solid ossicle, shifts in the position of F2 relative to the dorsal shell margin, and suppression of the development of F2.

2. Arenophilic glands occur in a wider range of taxa than previously thought. They are present in the most basal clade of extant anomalodesmatans (Pholadomyoidea) and presumably characterised the common ancestor of the crown group.

   Radial lines of secretion on the external surface of the shell allow the unequivocal identification of an arenophilic glandular system in species known only from conchological material. Because the system is exclusive of anomalodesmatans, recognition of this feature alone provides enough grounds for referral of taxa to the clade. Under exceptional conditions, arenophilic secretion is preserved in the fossil record.

3. Typical crossed-lamellar shell microstructure and combinations of nacreous with fined-grained layers occur in extant anomalodesmatans.

   Spikes, granules, brick-shaped elements and all other manifestations of periostracal calcification in anomalodesmatans are homologous. Suspicions of convergent evolution of these features based on apparently different modes of formation in either the mantle tissue or extra-pallial space find no support on empirical observations.

4. Radial slits through the umbonal sector of the shell wall, traditionally considered synapomorphies of a group joining laternulids and periplomatids, may have evolved iteratively in association to the deep-burrowing mode of life adopted by representatives of these families. Periplomatids share a more recent common ancestor with taxa classed in Thraciidae, Myochamidae and Cleidothaeridae, than they do with laternulids.

5. Clavagelloidea is monophyletic. Hence, the cryptic mode of life evolved only once within Anomalodesmata. Cementation of the valves to hard substrata evolved independently in clavagelloids, *Myochama* and *Cleidothaerus*.

6. Septibranchia is monophyletic and comprises the sister-group of a clade joining thraciids, periplomatids, myochamids and cleidothaerids. Similarities between parilimyids and septibranchs are due to convergence.

7. Monophyly of Pandoroidea and Thracioidea, previously rejected in molecular studies, is also refuted from a morphological perspective. Familial groups traditionally referred to these taxa are placed in two clades, one joining Lyonsiidae, Pandoridae, Laternulidae and Clavagelloidea ("lyonsiid" clade of Dreyer *et al.* 2003), and the other Thraciidae, Myochamidae, Cleidothaeridae and Periplomatidae ("thraciid" clade of Dreyer *et al.* 2003 with the addition of Periplomatidae).

   Pandoridae was recovered as the most basal anomalodesmatan branch from a morphological perspective, but is nevertheless included in the former clade based on stratigraphic and molecular evidence (Harper *et al.*, 2006).

8. The asymmetrical, subinternal ligament of ceratomyoids does not represent an intermediate stage between symmetrical external ligaments of pholadomyoids and the "sunken" internal ligaments supported by a calcified ossicle, which characterises most Cenozoic anomalodesmatans occupying shallow-burrowing and epifaunal modes of life. Ventral migration of the ligament, hitherto considered the most important evolutionary trend in the clade, finds no support in the ontogenesis of extant anomalodesmatans.

9. Interpreted in the light of the fossil record, the sister-group relationships of these shallow infaunal and epifaunal taxa suggest derivation from deep-burrowers, contradicting another earlier advanced pattern for the history of the clade — that of a slowly evolving stock of shallow-burrowers which would rapidly and irreversibly produce deep-burrowing forms.

   Instead, I envisage a split between two lineages of deep-burrowers early in the Mesozoic, which subsequently spawned shallow-burrowing and epifaunal taxa iter-

atively, probably via progenetic, small bodied species. In this context, the internal ligament supported by a sagittal lithodesma and the short siphons characteristic of these shallow infaunal and epifaunal taxa are interpreted as paedomorphic. Their resemblance to the early juvenile organs of deep-burrowing members of the "lyonsiid" and "thraciid" clades is thus explained.

References

Adal, M. N. & Morton, B. 1973. The fine structure of the pallial eyes of *Laternula truncata* (Bivalvia: Anomalodesmata: Pandoracea). *Journal of Zoology* **170**, 533–556.

Adamkewicz, S. L., Harasewych, M. G., Blake, J., Saudek, D. & Bult, C. J. 1997. A molecular phylogeny of the bivalve mollusks. *Molecular Biology and Evolution* **14**(6), 619–629.

Agnarsson, I. & Coddington, J. A. 2008. Quantitative tests of primary homology. *Cladistics* **24**(1), 51–61.

Agnarsson, I. & Miller, J. 2008. Is ACCTRAN better than DELTRAN? *Cladistics* **24**(6), 1032–1038.

Albrecht, G. H. & Gelvin, B. R. 1987. The simple allometry equation reconsidered: Assumptions, problems and alternative solutions. *American Journal of Physical Anthropology* **72**, 174.

Albrecht, G. H., Gelvin, B. R. & Hartman, S. E. 1993. Ratios as a size adjustment in morphometrics. *American Journal of Physical Anthropology* **91**(4), 441–468.

Allen, J. A. 1954. On the structure and adaptations of *Pandora inaequivalvis* and *P. pinna*. *Quarterly Journal of Microscopical Science, Third Series* **95**(4), 473–482.

Allen, J. A. 1958. Observations on *Cochlodesma praetenue* (Pulteney) Eulamellibranchia. *Journal of the Marine Biological Association of the United Kingdom* **37**, 97–112.

Allen, J. A. 1960*a*. The ligament of *Cochlodesma praetenue* (Pulteney). *Journal of the Marine Biological Association of the United Kingdom* **39**, 445–447.

Allen, J. A. 1960*b*. Manganese deposition on the shells of living molluscs. *Nature* **185**(4709), 336–337.

Allen, J. A. 1961*a*. The British species of *Thracia* (Eulamellibranchia). *Journal of the Marine Biological Association of the United Kingdom* **41**(3), 723–735.

Allen, J. A. 1961*b*. The development of *Pandora inaequivalvia* (Linné). *Journal of Embryology and Experimental Morphology* **9**, 252–268.

Allen, J. A. 1968. The functional morphology of *Crassinella mactracea* (Linsley) (Bivalvia: Astartacea). *Proceedings of the Malacological Society of London* **38**, 27–40.

Allen, J. A. 2008. Bivalvia of the deep Atlantic. *Malacologia* **50**(1–2), 57–174.

Allen, J. A. & Morgan, R. E. 1981. The functional morphology of Atlantic deep water species of the families Cuspidariidae and Poromyidae (Bivalvia): An analysis of the evolution of the septibranch condition. *Philosophical Transactions of the Royal Society of London, Series B* **294**(1073), 413–546.

Allen, J. A. & Turner, J. F. 1974. On the functional morphology of the family Verticordiidae (Bivalvia) with descriptions of new species from the abyssal Atlantic. *Philosophical Transactions of the Royal Society of London, Series B* **268**(894), 401–532.

Allen, M. F. & Allen, J. A. 1955. On the habits of *Pandora inaequivalvis* (Linné). *Proceedings of the Malacological Society of London* **31**, 175–185.

Aller, R. C. 1974. Prefabrication of shell ornamentation in the bivalve *Laternula*. *Lethaia* **7**(1), 43–56.

Allgaier, C. 2007. Active camouflage with lichens in a terrestrial snail, *Napaeus (N.) barquini* Alonso and Ibáñez, 2006 (Gastropoda, Pulmonata, Enidae). *Zoological Science* **24**(9), 869–876.

Amorim, D. d. S. 1997. *Elementos básicos de sistemática filogenética*. Editora Holos & Sociedade Brasileira de Entomologia, Ribeirão Preto, 2nd edition.

Ansell, A. D. 1961. The functional morphology of the British species of Veneracea (Eulamellibranchia). *Journal of the Marine Biological Association of the United Kingdom* **41**(2), 489–515.

Ansell, A. D. 1967. Burrowing in *Lyonsia norvegica* (Gmelin) (Bivalvia: Lyonsiidae). *Proceedings of the Malacological Society of London* **37**(6), 387–393.

Ansell, A. D. & Harvey, R. 1997. Protected larval development in the Antarctic bivalve *Laternula elliptica* (King & Broderip) (Anomalodesmata: Laternulidae). *Journal of Molluscan Studies* **63**, 285–286.

Astafieva-Urbaitis, K. A. 1970. Characteristics and systematic position of the bivalve genus *Edmondia*. *Paleontological Journal* **4**(3), 324–329.

Astafieva-Urbaitis, K. A. 1973. On the systematics of the Megadesmidae (Bivalvia). *Paleontological Journal* **7**(1), 9–14.

Atkins, D. 1937*a*. On the ciliary mechanisms and interrelationships of lamellibranchs. Part IV: Cuticular fusion, with special reference to the fourth aperture in certain lamellibranchs. *Quarterly Journal of Microscopical Science, New Series* **79**(3), 423–445.

Atkins, D. 1937*b*. On the ciliary mechanisms and interrelationships of lamellibranchs. Part III: Types of lamellibranch gills and their food currents. *Quarterly Journal of Microscopical Science, New Series* **79**(3), 375–421.

Atkins, D. 1937*c*. On the ciliary mechanisms and interrelationships of lamellibranchs. Part II: Sorting devices on the gills. *Quarterly Journal of Microscopical Science, New Series* **79**(315), 339–373.

Bailey, J. 1983. Middle Devonian Bivalvia from the Solsville Member (Marcellus Formation), central New York State. *Bulletin of the American Museum of Natural History* **174**(3), 193–326.

Bales, G. S. 1996. Heterochrony in brontothere horn evolution; allometric interpretations and the effect of life history scaling. *Paleobiology* **22**(4), 481–495.

Bambach, R. K. 1971. Adaptations in *Grammysia obliqua*. *Lethaia* **4**(2), 169–183.

Barash, A. & Danin, Z. 1972. The Indo-Pacific species of Mollusca in the Mediterranean and notes on a collection from the Suez canal. *Israel Journal of Zoology* **21**(3-4), 301–374.

Barón, P. J. & Ciocco, N. F. 1997. Anatomía de la almeja *Tellina petitiana* d'Orbigny, 1846. I. Organización general, valvas, manto, sifones, aductores, pie y branquias (Bivalvia, Tellinidae). *Revista de Biología Marina y Oceanografía* **32**(2), 95–110.

Baroni, C., Stenni, B. & Longinelli, A. 1991. Isotopic composition of Holocene shells from raised beaches and ice shelves of Terra Nova Bay (Victoria Land, Antarctica). *Memoire della Società Geologica Italiana* **46**, 93–102.

Beedham, G. E. 1958. Observations on the mantle of the Lamellibranchia. *Quaterly Journal of Microscopical Science, Third Series* **99**(2), 181–197.

Berges, J. A. 1997. Ratios, regression statistics, and "spurious" correlations. *Limnology and Oceanography* **42**(5), 1006–1007.

Bernard, F. 1895. Première note sur la développement et la morphologie de la coquille chez les lamellibranches. *Bulletin de la Société Géologique de France* **23**(3), 104–154.

Bernard, F. R. 1974. Septibranchs of the Eastern Pacific (Bivalvia Anomalodesmata). *Allan Hancock Monographs in Marine Biology* **8**, 1–279.

Bernard, F. R. 1979. New species of *Cuspidaria* from the Northeastern Pacific (Bivalvia : Anomalodesmata), with a proposed classification of septibranchs. *Venus* **38**(1), 14–24.

Bervian, G., Fontoura, N. & Haimovici, M. 2006. Statistical model of variable allometric growth: Otolith growth in *Micropogonias furnieri* (Actinopterygii, Sciaenidae). *Journal of Fish Biology* **68**(1), 196–208.

Bettencourt, V. & Guerra, A. 2000. Growth increments and biomineralization process in cephalopod statoliths. *Journal of Experimental Marine Biology and Ecology* **248**, 191–205.

Bhamrah, H. S. & Juneja, K. 2003. *Introduction to Mollusca.* Anmol Publications.

Bieler, R. & Mikkelsen, P. M., editors 1998. *Handbook of systematic malacology, part 3 (Scaphopoda / Bivalvia / Cephalopoda).* Smithsonian Institution Libraries and Amerind Publishing Company (Annotated English-language edition of: Thiele, J. Handbuch der systematischen Weichtierkunde, Teil 3).

Bieler, R. & Mikkelsen, P. M. 2006. Bivalvia — a look at the branches. In R. Bieler, editor, Bivalvia — a look at the branches. *Zoological Journal of the Linnean Society* **148**(3), 223–235.

Bigatti, G., Penchaszadeh, P. E. & Mercuri, G. 2001. Aspects of the gonadal cycle in the Antarctic bivalve *Laternula elliptica*. *Journal of Shellfish Research* **20**(7), 283–287.

Bøggild, O. B. 1930. The shell structure of the mollusks. *Kongelige Danske Videnskabernes Selskabs Skrifter, Naturvidenskabelig og Mathematisk, Afdeling* **2**, 235–326.

Boss, K. J. 1978. Taxonomic concepts and superfluity in bivalve nomenclature. In C. M. Yonge & T. E. Thompson, editors, Evolutionary systematics of bivalve molluscs. *Philosophical Transactions of the Royal Society of London, Series B* **284**(1001), 417–424.

Boss, K. J. 1982. Mollusca. In S. P. Parker, editor, *Synopsis and classification of living organisms*, volume 1, pages 945–1166. McGraw-Hill, New York.

Boss, K. J. & Merrill, A. S. 1965. The family Pandoridae in the Western Atlantic. *Johnsonia* **4**(44), 181–215.

Boyd, D. W. & Newell, N. D. 1969. Limitations of Bernard and Munier-Chalmas system for bivalve hinge notation. In R. C. Moore, editor, *Treatise on invertebrate paleontology.* Part N. Mollusca 6, Bivalvia, volume 1, pages N908–N913. Geological Society of America and University of Kansas Press.

Braithwaite, C. J. R., Taylor, J. D. & Glover, E. A. 2000. Marine carbonate cements, biofilms, biomineralization, and skeletogenesis: Some bivalves do it all. *Journal of Sedimentary Research* **70**(5), 1129–1138.

Bremer, K. 1994. Branch support and tree stability. *Cladistics* **10**(3), 295–304.

Broderip, W. 1835. On *Clavagella*. *Transactions of the Zoological Society of London* **1**, 261–268.

Bryant, H. N. 2001. Character polarity and the rooting of cladograms. In G. P. Wagner, editor, *The character concept in evolutionary biology*, pages 319–338. Academic Press, New York.

Burne, R. H. 1920. Mollusca. Part IV. Anatomy of Pelecypoda. *British Antarctic ("Terra Nova") Expedition, 1910, Natural History Report, Zoology* **2**(10), 233–256.

Campbell, D. C. 2000. Molecular evidence on the evolution of the Bivalvia. In E. M. Harper, J. D. Taylor & J. A. Crame, editors, The evolutionary biology of the Bivalvia. *Geological Society, London, Special Publications* **177**, 31–46.

Carter, J. G. 1978. Ecology and evolution of the Gastrochaenacea, with notes on the evolution of the endolithic habit. *Bulletin of the Peabody Museum of Natural History* **41**, 1–92.

Carter, J. G. 1990. Evolutionary significance of shell microstructure in the Paleotaxodonta, Pteriomorphia and Isofilibranchia (Bivalvia: Mollusca). In J. G. Carter, editor, *Skeletal biomineralization: Patterns, processes, and evolutionary trends*, volume 1, pages 135–296. Van Nostrand Reinhold, New York.

Carter, J. G. & Aller, R. C. 1975. Calcification in the bivalve periostracum. *Lethaia* **8**, 315–320.

Carter, J. G., Campbell, D. C. & Campbell, M. R. 2000. Cladistic perspectives on early bivalve evolution. In E. M. Harper, J. D. Taylor & J. A. Crame, editors, The evolutionary biology of the Bivalvia. *Geological Society, London, Special Publications* **177**, 31–46.

Carter, J. G. & Clark II, G. R. 1985. Classification and phylogenetic significance of molluscan shell microstructure. In T. W. Broadhead, editor, Mollusks: Notes for a short course. *University of Tennesse Department of Geological Sciences Study in Geology* **13**, 50–71.

Carter, J. G. & Tevesz, M. J. S. 1978. Shell microstructure of a Middle Devonian (Hamilton group) bivalve fauna from central New York. *Journal of Paleontology* **52**(4), 859–880.

Chanley, P. & Castagna, M. 1966. Larval development of the pelecypod *Lyonsia hyalina*. *Nautilus* **79**(4), 123–128.

Checa, A. & Rodriguez-Navarro, A. 2001. Geometrical and crystallographic constraints determine the self-organization of shell microstructures in Unionidae (Bivalvia: Mollusca). *Proceedings of the Royal Society of London, Series B* **268**(1468), 771–778.

Checa, A. G. & Cadée, G. C. 1997. Hydraulic burrowing in the bivalve *Mya arenaria* Linnaeus (Myoidea) and associated ligamental adaptations. *Journal of Molluscan Studies* **63**, 157–171.

Chinzei, K., Savazzi, E. & Seilacher, A. 1982. Adaptational strategies of bivalves living as infaunal secondary soft bottom dwellers. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **164**, 229–244.

Coan, E. V. 1990*a*. The Eastern Pacific species of the bivalve family Spheniopsidae. *Veliger* **33**, 394–401.

Coan, E. V. 1990*b*. The Recent Eastern Pacific species of the bivalve family Thraciidae. *Veliger* **33**(1), 20–55.

Coan, E. V., Valentich-Scott, P. & Bernard, F. R. 2000. *Bivalve seashells of Western North America: Marine bivalve mollusks from Arctic Alaska to Baja California.* Santa Barbara Museum of Natural History Monographs Number 2; Studies in Biodiversity Number 2. Santa Barbara Museum of Natural History, Santa Barbara.

Cope, J. C. W. 1996*a*. Early Ordovician (Arenig) bivalves from the Llangynog Inlier, South Wales. *Palaeontology* **39**, 979–1025.

Cope, J. C. W. 1996*b*. The early evolution of the Bivalvia. In J. D. Taylor, editor, *Origin and evolutionary radiation of the Mollusca*, pages 361–370. Oxford University Press, Oxford.

Cope, J. C. W. 1997. The early phylogeny of the class Bivalvia. *Palaeontology* **40**(3), 713–746.

Cox, L. R. 1960. Thoughts on the classification of the Bivalvia. *Proceedings of the Malacological Society of London* **34**(2), 60–88.

Cox, L. R. 1963. The Rhaetic-Hettangian bivalve genus *Pteromya* Moore. *Palaeontology* **6**(3), 582–595.

Cox, L. R. 1969*a*. Family Ceratomyidae Arkell, 1934. In R. C. Moore, editor, *Treatise on invertebrate paleontology.* Part N. Mollusca 6, Bivalvia, volume 2, pages N838–N841. Geological Society of America and University of Kansas Press.

Cox, L. R. 1969*b*. Family Myopholadidae Cox, 1964. In R. C. Moore, editor, *Treatise on invertebrate paleontology.* Part N. Mollusca 6, Bivalvia, volume 2, pages N841–N842. Geological Society of America and University of Kansas Press.

Cox, L. R. 1969*c*. Family Pleuromyidae Dall, 1900. In R. C. Moore, editor, *Treatise on invertebrate paleontology.* Part N. Mollusca 6, Bivalvia, volume 2, pages N842–N843. Geological Society of America and University of Kansas Press.

Cox, L. R. & Newell, N. D. 1969. Family Pholadomyidae Gray, 1847. In R. C. Moore, editor, *Treatise on invertebrate paleontology.* Part N. Mollusca 6, Bivalvia, volume 2, pages N827–N838. Geological Society of America and University of Kansas Press.

Cox, L. R., Nuttall, C. P. & Trueman, E. R. 1969. General features of Bivalvia. In R. C. Moore, editor, *Treatise on invertebrate paleontology.* Part N. Mollusca 6, Bivalvia, volume 1, pages N2–N129. Geological Society of America and University of Kansas Press.

Dall, W. H. 1886*a*. Neæra. *Nature* **34**, 122.

Dall, W. H. 1886*b*. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78) and in the Caribbean Sea (1879-80), by the U. S. Coast Survey steamer "Blake", Lieut.-Commander C. D. Sigsbee, U. S. N., and Commander J. R. Bartlett, U. S. N., commanding. XXIX. Report on the Mollusca — part 1. Brachiopoda and Pelecypoda. *Bulletin of the Museum of Comparative Zoology* **12**(6), 171–318.

Dall, W. H. 1889*a*. On the hinge of pelecypods and its development, with an attempt toward a better subdivision of the group. *American Journal of Science* **38**, 445–462.

Dall, W. H. 1889*b*. Addenda and corrigenda to part 1, 1886. In Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78) and in the Caribbean Sea (1879-80), by the U. S. Coast Survey steamer "Blake", Lieut.-Commander C. D. Sigsbee, U. S. N., and Commander J. R. Bartlett, U. S. N., commanding. XXIX — Report on the Mollusca. Part II — Gastropoda and Scaphopoda. *Bulletin of the Museum of Comparative Zoology* **18**, 433–452.

Dall, W. H. 1895. Contributions to the Tertiary fauna of Florida with especial reference to the Miocene silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River. Part III. A new classification of the Pelecypoda. *Transactions of the Wagner Free Institute of Science (Philadelphia)* **3**, 483–565.

Dall, W. H. 1895. Scientific results of explorations by the U. S. Fish Commission steamer Albatross. XXXIV — Report on Mollusca and Brachiopoda dredged in deep water, chiefly near the Hawaiian Islands with illustrations of hitherto unfigured species from Northwest America. *Proceedings of the United States National Museum* **17**(1032), 675–733.

Dall, W. H. 1903. Contributions to the Tertiary fauna of Florida with especial reference to the silex beds of Tampa and the Pliocene beds of the Caloosahatchie River including in many cases a complete revision of the generic groups treated of and their American Tertiary species. Part VI. Concluding the work. *Transactions of the Wagner Free Institute of Science (Philadelphia)* **3**(6), 1–14 and 1219–1654.

Dall, W. H. 1913. Pelecypoda. In K. A. von Zittel translated and edited by C. R. Eastman, editor, *Text-book of palaeontology*, volume 1, pages 422–507.

Dall, W. H. 1917. Diagnoses of new species of marine bivalve mollusks from the Northwest coast of America in the collection of the United States National Museum. *Proceedings of the United States National Museum of Natural History* **52**, 393–417.

Dance, S. P. 1969. *Rare shells*. Faber and Faber Limited, London.

Dell, R. K. 1990. Antarctic Mollusca with special reference to the fauna of the Ross Sea. *Bulletin of the Royal Society of New Zealand* **27**, 1–311.

Denadai, M. R., Amaral, A. C. Z. & Turra, A. 2001. Spatial distribution of molluscs on sandy intertidal substrates with rock fragments in South-Eastern Brazil. *Estuarine, Coastal and Shelf Science* **53**(5), 733–743.

Deshayes, G. P. 1845–1848. Histoire naturelle des mollusques, vol. 1. Mollusques acéphalés. In *Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842 publieé par ordre du gouvernement et avec le concours d'une commission académique. Sciences physiques. Zoologie*, xx + 609 pages. Imprimerie Nationale, Paris.

Diaz, J. M., Gast, F. & Torres, D. C. 2009. Rediscovery of a Caribbean living fossil: *Pholadomya candida* G.B. Sowerby I, 1823 (Bivalvia: Anomalodesmata: Pholadomyoidea). *Nautilus* **123**(1), 19–20.

Dick, D., Philipp, E., Kriews, M. & Abele, D. 2007. Is the umbo matrix of bivalve shells (*Laternula elliptica*) a climate archive? *Aquatic Toxicology* **84**(4), 450–456.

Dickins, J. M. 1963. Permian pelecypods and gastropods from Western Australia. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics* **63**, 1–203.

Dinamani, P. 1967. Variation in the stomach structure of the Bivalvia. *Malacologia* **5**, 225–268.

Domaneschi, O. & Shea, E. K. 2004. Shell morphometry of Western Atlantic and Indo-West Pacific *Asaphis*; functional morphology and ecological aspects of *A. deflorata* from Florida Keys, U.S.A. (Bivalvia: Psammobiidae). In R. Bieler & P. M. Mikkelsen, editors, Bivalve studies in the Florida Keys: Proceedings of the International Marine Bivalve Workshop, Long Key, Florida, July 2002. *Malacologia* **46**(2), 249–275.

Dreyer, H., Steiner, G. & Harper, E. M. 2003. Molecular phylogeny of Anomalodesmata (Mollusca: Bivalvia) inferred from 18S rRNA sequences. *Zoological Journal of the Linnean Society* **139**, 229–246.

Duval 1963. The comparative anatomy of some lamellibranch siphons. *Proceedings of the Malacological Society of London* **35**, 289–295.

Evseev, G. A., Kolotukhina, N. K. & Semenikhina, O. Y. 2001. Shell morphogenesis of several venerid bivalves. *Journal of Shellfish Research* **20**(3), 1279–1284.

Evseev, G. A., Semenikhina, O. Y. & Kolotukhina, N. K. 2004. Shell morphogenesis of *Alveinus ojianus* (Bivalvia: Kelliellidae) and taxonomic significance of the early features. *Journal of Molluscan Studies* **70**(4), 319–328.

Fang, Z. & Morris, N. J. 1997. The genus *Pseudosanguinolites* and some modioliform bivalves (mainly Palaeozoic). *Palaeoworld* **7**, 49–74.

Farris, J. S. 1990. Phenetics in camouflage. *Cladistics* **6**(1), 91–100.

Feener, D. H., J., Lighton, J. R. B. & Bartholomew, G. A. 1988. Curvilinear allometry, energetics and foraging ecology: a comparison of leaf-cutting ants and army ants. *Functional Ecology* **2**(4), 509–520.

Fishelson, L. 2000. Comparative morphology and cytology of siphons and siphonal sensory organs in selected bivalve molluscs. *Marine Biology* **137**, 497–509.

Forbes, E. & Hanley, S. 1853. *A history of the British Mollusca and their shells. Volume I. Including the Tunicata, and the families of Lamellibranchiata as far as Cyprinidae.* John Van Voorst, London.

Frith, D. W., Tantanasiriwong, R. & Bhatia, O. 1976. Zonation and abundance of macrofauna on a mangrove shore, Phuket Island. *Phuket Marine Biological Center Research Bulletin* **10**, 1–37.

Gibson-Smith, J. & Gibson-Smith, W. 1981. The status of *Pholadomya candida* G. B. Sowerby, I, 1823. *Veliger* **23**, 355–356.

Giribet, G. 2007. Efficient tree searches with available algorithms. *Evolutionary Bioinformatics* **2007**(3), 341–356.

Giribet, G. 2008. Bivalvia. In W. F. Ponder & D. R. Lindberg, editors, *Phylogeny and evolution of the Mollusca*, pages 105–141. University of California Press, Berkeley.

Giribet, G. & Distel, D. L. 2003. Bivalve phylogeny and molecular data. In C. Lydeard & D. R. Lindberg, editors, *Molecular systematics and phylogeography of mollusks*, pages 45–90. Smithsonian Books, Washington, DC.

Giribet, G. & Wheeler, W. 2002. On bivalve phylogeny: A high-level analysis of the Bivalvia (Mollusca) based on combined morphology and DNA sequence data. *Invertebrate Biology* **121**(4), 271–324.

Goloboff, P. A. 1999. Analysing large data sets in reasonable time: Solutions for composite optima. *Cladistics* **15**, 415–428.

Goloboff, P. A. 2002. Techniques for analysing large data sets. In R. DeSalle, G. Giribet & W. C. Wheeler, editors, *Techniques in molecular systematics and evolution*, pages 70–79. Birkhäuser Basel.

Goloboff, P. A., Farris, J. S. & Nixon, K. C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* **24**(5), 774–786.

Goloboff, P. A., Mattoni, C. I. & Quinteros, A. S. 2006. Continuous characters analyzed as such. *Cladistics* **22**(6), 589–601.

Goodsell, J. G., Fuller, S. C., Eversole, A. G., Castagna, M. & Lutz, R. A. 1992. Larval and early postlarval shell morphology of several venerid clams. *Journal of the Marine Biological Association of the United Kingdom* **72**(1), 231–255.

Gould, S. J. 1966. Allometry and size in ontogeny and phylogeny. *Biological Reviews* **41**(4), 587–638.

Gould, S. J. 1971. Geometric similarity in allometric growth: A contribution to the problem of scaling in the evolution of size. *American Naturalist* **105**(942), 113–136.

Gould, S. J. 1977. *Ontogeny and phylogeny*. Belknap Press of Harvard University Press Cambridge, Mass.

Graf, D. L. & Cummings, K. S. 2006. Palaeoheterodont diversity (Mollusca: Trigonioida + Unionoida): What we know and what we wish we knew about freshwater mussel evolution. In R. Bieler, editor, Bivalvia — a look at the branches. *Zoological Journal of the Linnean Society* **148**(3), 343–394.

Graham, A. 1949. The molluscan stomach. *Transactions of the Royal Society of Edinburgh* **61**(27), 737–778.

Gustafson, R. G., Ó Foighil, D. & Reid, R. G. 1986. Early ontogeny of the septibranch bivalve *Cardiomya pectinata* (Carpenter, 1865). *Journal of the Marine Biological Association of the United Kingdom* **66**(4), 943–950.

Hancock, A. 1853*a*. On the animal of *Chamostrea albida*. *Annals and Magazine of Natural History, Second Series* **11**(62), 106–112.

Hancock, A. 1853*b*. On the animal of *Myochama anomioides*. *Annals and Magazine of Natural History, Second Series* **11**(64), 287–291.

Harper, E. M. 1997. The molluscan periostracum: An important constraint in bivalve evolution. *Palaeontology* **40**(1), 71–97.

Harper, E. M., Checa, A. G. & Rodríguez-Navarro, A. B. 2009. Organization and mode of secretion of the granular prismatic microstructure of *Entodesma navicula* (Bivalvia: Mollusca). *Acta Zoologica* **90**, 132–141.

Harper, E. M., Dreyer, H. & Steiner, G. 2006. Reconstructing the Anomalodesmata (Mollusca: Bivalvia): Morphology and molecules. In R. Bieler, editor, Bivalvia — a look at the branches. *Zoological Journal of the Linnean Society* **148**(3), 395–420.

Harper, E. M., Hide, E. A. & Morton, B. 2000. Relationships between the extant Anomalodesmata: A cladistic test. In E. M. Harper, J. D. Taylor & J. A. Crame, editors, The evolutionary biology of the Bivalvia. *Geological Society, London, Special Publications* **177**, 129–143.

Harper, E. M. & Morton, B. 2000. The biology and functional morphology of *Myochama anomioides* Stutchbury, 1830 (Bivalvia: Anomalodesmata: Pandoroidea) with reference to cementation. *Journal of Molluscan Studies* **66**, 403–416.

Harper, E. M. & Morton, B. 2004. Tube construction in the watering pot shell *Brechites vaginiferus* (Bivalvia; Anomalodesmata; Clavagelloidea). *Acta Zoologica* **85**, 149–161.

Harper, E. M., Palmer, T. J. & Hudson, J. D. 2002. The Middle Jurassic bivalve *'Cuspidaria' ibbetsoni*: A corbulid not a septibranch. *Palaeontology* **45**(4), 759–769.

Harper, E. M. & Peck, L. 2003. Predatory behaviour and metabolic costs in the Antarctic muricid gastropod *Trophon longstaffi*. *Polar Biology* **26**, 208–217.

Harte, M. E. 1998. Superfamily Veneroidea. In P. L. Beesley, G. J. B. Ross & A. Wells, editors, *Mollusca: The southern synthesis. Fauna of Australia*, volume 5, Part A, pages 355–362. CSIRO Publishing, Melbourne.

Hawkins, J. A., Hughes, C. E. & Scotland, R. W. 1997. Primary homology assessment, characters and character states. *Cladistics* **13**(3), 275–283.

Healey, M. 1908. The fauna of the Napeng beds or the Rhaetic beds of Upper Burma. *Memoirs of the Geological Survey of India, Palaeontologia Indica* **2**(4), 1–88.

Healy, J. M. 1996. Molluscan sperm ultrastructure: Correlation with taxonomic units within the Gastropoda, Cephalopoda and Bivalvia. In J. D. Taylor, editor, *Origin and evolutionary radiation of the Mollusca*, pages 99–113. Oxford University Press, Oxford.

Healy, J. M., Bieler, R. & Mikkelsen, P. M. 2008. Spermatozoa of the Anomalodesmata (Bivalvia, Mollusca) with special reference to relationships within the group. *Acta Zoologica* **89**(4), 339–350.

Hedegaard, C. 1997. Shell structures of the Recent Vetigastropoda. *Journal of Molluscan Studies* **63**(3), 369–377.

Hedegaard, C. & Wenk, H.-R. 1998. Microstructure and texture patterns of mollusc shells. *Journal of Molluscan Studies* **64**(1), 133–136.

Hedley, C. 1904. Studies on Australian Mollusca. Part VIII. *Proceedings of the Linnean Society of New South Wales* **29**, 182–212.

Hennig, W. 1966. *Phylogenetic systematics*. University of Illinois Press, Urbana.

Hillman, R. E. & Shuster Jr, C. N. 1966. A comment on the origin of the fourth fold in the mantle of the quahog, *Mercenaria mercenaria*. *Chesapeake Science* **7**, 112–113.

Hodgson, A. N. & Fielden, L. J. 1984. The structure and distribution of peripheral ciliated receptors in the bivalve molluscs *Donax serra* and *D. sordidus*. *Journal of Molluscan Studies* **50**, 104–112.

Hodgson, A. N. & Fielden, L. J. 1986. The ultrastructure of ciliated cells from the siphon of *Solen capensis* (Mollusca, Bivalvia). *Journal of Molluscan Studies* **52**, 161–168.

Huxley, J. S. 1932. *Problems of relative growth*. Dover, New York, 1st edition.

Iredale, T. 1924. Results from Roy Bell's molluscan collections. *Proceedings of the Linnean Society of New South Wales* **49**, 179–278.

Johnston, P. A. 1993. Lower Devonian Pelecypoda from Southeastern Australia. *Association of Australasian Palaeontologists, Memoir* **14**, 1–134.

Jones, D. S. & Nicol, D. 1989. Eocene clavagellids (Mollusca: Pelecypoda) from Florida: The first documented occurrence in the Cenozoic of the Western Hemisphere. *Journal of Paleontology* **63**(3), 320–323.

Kamenev, G. M. 2002. Genus *Parvithracia* (Bivalvia: Thraciidae) with descriptions of a new subgenus and two new species from the Northwestern Pacific. *Malacologia* **44**(1), 107–134.

Kamenev, G. M. & Nadtochy, V. A. 1998. Two new species of *Lampeia* (Bivalvia: Thraciidae) from the Northwestern Pacific, with notes on *Lampeia adamsi* (MacGinitie, 1959). *Veliger* **41**(3), 259–273.

Keen, A. M. 1969*a*. Superfamily Poromyacea Dall, 1886. In R. C. Moore, editor, *Treatise on invertebrate paleontology*. Part N. Mollusca 6, Bivalvia, volume 2, pages N852–N857. Geological Society of America and University of Kansas Press.

Keen, A. M. 1969*b*. Superfamily Pandoracea Rafinesque, 1815. In R. C. Moore, editor, *Treatise on invertebrate paleontology*. Part N. Mollusca 6, Bivalvia, volume 2, pages N843–N852. Geological Society of America and University of Kansas Press.

Keen, A. M. 1969*c*. Family Margaritariidae Vokes, 1964. In R. C. Moore, editor, *Treatise on invertebrate paleontology*. Part N. Mollusca 6, Bivalvia, volume 2, page N847. Geological Society of America and University of Kansas Press.

Keen, A. M. & Smith, L. A. 1969. Superfamily Clavagellacea d'Orbigny, 1844. In R. C. Moore, editor, *Treatise on invertebrate paleontology*. Part N. Mollusca 6, Bivalvia, volume 2, pages N857–N859. Geological Society of America and University of Kansas Press.

Kennedy, W. J. & Hall, A. 1967. The influence of organic matter on the preservation of aragonite in fossils. *Proceedings of the Geological Society of London* **1643**, 253–255.

Klingenberg, C. P. 1998. Heterochrony and allometry: The analysis of evolutionary change in ontogeny. *Biological Reviews* **73**(1), 79–123.

Knudsen, J. 1967. The deep-sea Bivalvia. *Scientific Reports of the John Murray Expedition 1933–34* **11**(3), 237–343.

Knudsen, J. 1970. The systematics and biology of abyssal and hadal Bivalvia. *Galathea Report* **11**, 7–236.

de Koninck, L.-G. 1844. *Description des animaux fossiles qui se trouvent dans le terrain Carbonifère de Belgique*. H. Dessain, Liège.

Krug, A. Z., Jablonski, D. & Valentine, J. W. 2007. Contrarian clade confirms the ubiquity of spatial origination patterns in the production of latitudinal diversity gradients. *Proceedings of the National Academy of Sciences* **104**(46), 18129–18134.

Krylova, E. M. 2001. Septibranchiate molluscs of the family Poromyidae (Bivalvia: Poromyoidea) from the tropical Western Pacific Ocean. In P. Bouchet & B. A. Marshall, editors, Tropical deep-sea benthos 22. *Mémoires du Muséum National d'Histoire Naturelle* **185**, 165–200.

Krylova, E. M. 2006. Bivalves of the seamounts of the North-Eastern Atlantic. Part 1. In A. N. Mironov, A. V. Gebruk & A. J. Southward, editors, *Biogeography of the north atlantic seamounts: Collected proceeding*, pages 76–97. KMK Scientific Press, Moscow.

Kubo, M. 1977. The formation of a temporary-acrosome in the spermatozoon of *Laternula limicola* (Bivalvia, Mollusca). *Journal of Ultrastructure Research* **61**(1), 140–148.

Kubo, M. & Ishikawa, M. 1978. Organizing process of the temporary acrossome in spermatogenesis of the bivalve *Lyonsia ventricosa*. *Journal of Submicroscopic Cytology* **10**(4), 411–421.

LaBarbera, M. 1974. Larval and post-larval development of five species of Miocene bivalves (Mollusca). *Journal of Paleontology* **48**(2), 256–277.

LaBarbera, M. 1989. Analyzing body size as a factor in ecology and evolution. *Annual Review of Ecology and Systematics* **20**(1), 97–117.

Lacaze-Duthiers, H. 1883. Morphologie des acéphales. Premier mémoire. Anatomie de l'arrosoir (*Aspergillum dichotomum*, L. Reeve). *Archives de Zoologie Expérimentale et générale, Deuxième Série* **1**, 665–732.

Lagergren, R., Svensson, J.-E. & Stenson, J. 2007. Models of ontogenetic allometry in cladoceran morphology studies. *Hydrobiologia* **594**(1), 109–116.

Lammens, J. J. 1968. The morphology of the central nervous system of *Macoma balthica* (L.). *Netherlands Journal of Zoology* **19**(1), 105–127.

LaRocque, A. & Newell, N. D. 1969. Superfamily Modiomorphacea Miller, 1877. In R. C. Moore, editor, *Treatise on invertebrate paleontology*, volume N of *Mollusca 6, Bivalvia*, pages N393–N399. Geological Society of America and University of Kansas Press.

Lazo, D. G. 2007. The bivalve *Pholadomya gigantea* in the Early Cretaceous of Argentina: Taxonomy, taphonomy and paleogeographic implications. *Acta Palaeontologica Polonica* **52**(2), 375–390.

Le Pennec, M. 1973. Morphogenèse de la charnière chez 5 espèces de Veneridae. *Malacologia* **12**, 225–245.

Le Pennec, M. & Jüngbluth, J. H. 1983. The ligamental formations of *Margaritifera margaritifera* (L.) (Bivalvia: Margaritiferidae) and *Mytilus edulis* (L.) (Bivalvia: Mytilidae) during larval and postlarval ontogenesis. *Journal of the Marine Biological Association of the United Kingdom* **63**, 289–294.

Leal, J. H. 2008. A remarkable new genus of carnivorous, sessile bivalves (Mollusca: Anomalodesmata: Poromyidae) with descriptions of two new species. *Zootaxa* **1764**, 1–18.

Linsley, R. M. & Yochelson, E. L. 1973. Devonian carrier shells (Euomphalidae) from North America and Germany. *United States Geological Survey Professional Paper* **824**, 1–26.

Lourido, A., Gestoso, L. & Troncoso, J. S. 2006. Assemblages of the molluscan fauna in subtidal soft bottoms of the Ría de Aldán (North-Western Spain). *Journal of the Marine Biological Association of the United Kingdom* **86**, 129–140.

Lutz, R. A., Mann, R., Goodsell, J. G. & Castagna, M. 1982. Larval and early postlarval development of *Arctica islandica*. *Journal of the Marine Biological Association of the United Kingdom* **62**(4), 745–769.

Maddison, D. R. & Maddison, W. P. 2005. *MacClade 4: Analysis of phylogeny and character evolution. version 4.08*. Sinauer Associates, Sunderland, Massachusetts.

Maddison, W. 1989. Reconstructing character evolution on polytomous cladograms. *Cladistics* **5**(4), 365–377.

Malchus, N. 2004. Constraints in the ligament ontogeny and evolution of pteriomorphian Bivalvia. *Palaeontology* **47**(6), 1539–1574.

Malchus, N. 2005. The riddle of bivalve ligament homology. *Notiziario S.I.M. 23(5-8): 10. Secondo Supplemento del Bolletino Malacologico* **41**(1-4).

Marsh, L. F. 1984. Mode of life and autecology of Silurian–Devonian Grammysiidae (Bivalvia). *Palaeontology* **27**(4), 679–691.

Marshall, B. A. 2002. Some Recent Thraciidae, Periplomatidae, Myochamidae, Cuspidariidae and Spheniopsidae (Anomalodesmata) from the New Zealand region and referral of *Thracia reinga* Crozier, 1966 and *Scintillona benthicola* Dell, 1956 to *Tellimya* Brown, 1827 (Montacutidae) (Mollusca : Bivalvia). *Molluscan Research* **22**, 221–288.

McKinney, M. L. & McNamara, K. J. 1991. *Heterochrony: The evolution of ontogeny.* Plenum Press, New York.

Mercuri, G., Iken, K., Ledesma, B. & Dubois, R. F. 1998. On the distribution patterns and density of the Antarctic infaunal bivalve *Laternula elliptica* in Potter Cove, King George Island, Antarctica. *Berichte zur Polarforschung (Reports on Polar Research)* **299**, 137–143.

Mikkelsen, P. M. & Bieler, R. 2008. *Seashells of Southern Florida: Living marine mollusks of the Florida Keys and adjacent regions. Bivalves.* Princeton University Press, Princeton.

Mikkelsen, P. M., R. Bieler, I. K. & Rawlings, T. A. 2006. Phylogeny of Veneroidea (Mollusca: Bivalvia) based on morphology and molecules. In R. Bieler, editor, Bivalvia — a look at the branches. *Zoological Journal of the Linnean Society* **148**(3), 439–521.

Morley, S. A., Peck, L. S., Tan, K. S., Martin, S. M. & Pörtner, H. O. 2007. Slowest of the slow: Latitudinal insensitivity of burrowing capacity in the bivalve *Laternula*. *Marine Biology* **151**(5), 1823–1830.

Morris, N. J., Dickins, J. M. & Astafieva-Urbaitis, K. 1991. Upper Palaeozoic anomalodesmatan bivalves. *Bulletin of the British Museum of Natural History (Geology Series)* **47**(1), 51–100.

Morton, B. 1973*a*. The biology and functional morphology of *Laternula truncata* (Lamarck, 1818) (Bivalvia: Anomalodesmata: Pandoracea). *Biological Bulletin* **145**(3), 509–531.

Morton, B. 1973*b*. A new theory of feeding and digestion in the filter-feeding Lamellibranchia. *Malacologia* **14**, 63–79.

Morton, B. 1974. Some aspects of the biology and functional morphology of *Cleidothaerus maorianus* Finlay (Bivalvia: Anomalodesmata: Pandoracea). *Proceedings of the Malacological Society of London* **41**(3), 201–222.

Morton, B. 1976. The structure, mode of operation and variation in form of the shell of the Laternulidae (Bivalvia: Anomalodesmata: Pandoracea). *Journal of Molluscan Studies* **42**, 261–278.

Morton, B. 1977. Some aspects of the biology and functional morphology of *Myadora striata* (Quoy & Gaimard) (Bivalvia: Anomalodesmata: Pandoracea). *Journal of Molluscan Studies* **43**, 141–154.

Morton, B. 1980. Anatomy of the living fossil *Pholadomya candida* Sowerby 1823 (Bivalvia: Anomalodesmata: Pholodomyacea). *Vindenskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjobenhavn* **142**, 7–101.

MORTON, B. 1981*a*. The biology and functional morphology of *Periploma (Offadesma) angasai* (Bivalvia: Anomalodesmata: Periplomatidae). *Journal of Zoology* **193**(1), 39–70.

MORTON, B. 1981*b*. The Anomalodesmata. *Malacologia* **21**(1–2), 35–60.

MORTON, B. 1981*c*. Prey capture in the carnivorous septibranch *Poromya granulata* (Bivalvia: Anomalodesmata: Poromyacea). *Sarsia* **66**, 241–256.

MORTON, B. 1982. The functional morphology of *Parilimya fragilis* (Bivalvia: Parilimyidae nov. fam.) with a discussion on the origin and evolution of the carnivorous septibranchs and a reclassification of the Anomalodesmata. *Transactions of the Zoological Society of London* **36**(3), 153–216.

MORTON, B. 1984*a*. The biology and functional morphology of *Clavagella australis* (Bivalvia: Anomalodesmata). *Journal of Zoology* **202**, 489–511.

MORTON, B. 1984*b*. Adventitious tube construction in *Brechites vaginiferus* (Bivalvia: Anomalodesmata: Clavagellacea) with an investigation of the juvenile of *Humphreyia strangei*. *Journal of Zoology* **204**, 461–484.

MORTON, B. 1984*c*. Prey capture in *Lyonsiella formosa* (Bivalvia: Anomalodesmata: Verticordiacea). *Pacific Science* **38**(4), 283–297.

MORTON, B. 1984*d*. The adaptations of *Frenamya ceylanica* (Bivalvia: Anomalodesmata: Pandoracea) to life on surface of soft muds. *Journal of Conchology* **31**(6), 359–371.

MORTON, B. 1985*a*. Adaptive radiation in the Anomalodesmata. In E. R. Trueman & M. N. Clarke, editors, *The Mollusca*, volume 10 (Evolution), pages 405–459. Academic Press, Orlando.

MORTON, B. 1985*b*. Statocyst structure in the Anomalodesmata (Bivalvia). *Journal of Zoology (Series A)* **206**, 23–34.

MORTON, B. 1987*a*. Siphon structure and prey capture as a guide to affinities in the abyssal septibranch Anomalodesmata (Bivalvia). *Sarsia* **72**, 49–69.

MORTON, B. 1987*b*. The mantle margin and radial mantle glands of *Entodesma saxicola* and *E. inflata* (Bivalvia: Anomalodesmata: Lyonsiidae). *Journal of Molluscan Studies* **53**(2), 139–151.

MORTON, B. 1987*c*. The functional morphology of *Neotrigonia margaritacea* (Bivalvia: Trigoniacea) with a discussion of phylogenetic affinities. *Records of the Australian Museum* **39**, 339–354.

MORTON, B. 1995. The ecology and functional morphology of *Trigonothracia jinxingae* (Bivalvia: Anomalodesmata: Thracioidea) from Xiamen, China. *Journal of Zoology* **237**(3), 445–468.

MORTON, B. 1996. The evolutionary history of the Bivalvia. In J. D. Taylor, editor, *Origin and evolutionary radiation of the Mollusca*, pages 337–359. Oxford University Press, Oxford.

MORTON, B. 2002*a*. Biology and functional morphology of the watering pot shell *Brechites vaginiferus* (Bivalvia: Anomalodesmata: Clavagelloidea). *Journal of Zoology* **257**, 545–562.

MORTON, B. 2002*b*. The biology and functional morphology of *Humphreyia strangei* (Bivalvia: Anomalodesmata: Clavagellidae): An Australian cemented 'watering pot' shell. *Journal of Zoology* **258**, 11–25.

MORTON, B. 2003*a*. The biology and functional morphology of *Dianadema* gen. nov. *multangularis* (Tate, 1887) (Bivalvia: Anomalodesmata: Clavagellidae). *Journal of Zoology* **259**, 389–401.

MORTON, B. 2003*b*. The functional morphology of *Bentholyonsia teramachii* (Bivalvia: Lyonsiellidae): Clues to the origin of predation in the deep water Anomalodesmata. *Journal of Zoology* **261**, 363–380.

MORTON, B. 2004*a*. The biology and functional morphology of *Nipponoclava gigantea*: Clues to the evolution of tube dwelling in the Penicillidae (Bivalvia: Anomalodesmata: Clavagelloidea). *Journal of Zoology* **264**, 355–369.

MORTON, B. 2004*b*. Biology and functional morphology of *Kendrickiana* gen. nov *veitchi* (Bivalvia : Anomalodesmata : Clavagelloidea) from Southern Australia. *Invertebrate Biology* **123**(3), 244–259.

MORTON, B. 2004*c*. The biology and functional morphology of *Foegia novaezelandiae* (Bivalvia: Anomalodesmata: Clavagelloidea) from Western Australia. *Malacologia* **46**(1), 37–55.

MORTON, B. 2005. Biology and functional morphology of a new species of endolithic *Bryopa* (Bivalvia : Anomalodesmata : Clavagelloidea) from Japan and a comparison with fossil species of *Stirpulina* and other Clavagellidae. *Invertebrate Biology* **124**(3), 202–219.

MORTON, B. 2006*a*. Structure and formation of the adventitious tube of the Japanese watering-pot shell *Stirpulina ramosa* (Bivalvia, Anomalodesmata, Clavagellidae) and a comparison with that of the Penicillidae. *Invertebrate Biology* **125**(3), 233–249.

MORTON, B. 2006*b*. The functional morphology of *Penicillus philippinensis* (Anomalodesmata: Clavagelloidea: Penicillidae) and the evolution of an unique muscular system in the Bivalvia. *Records of the Western Australian Museum* **23**(2), 175–191.

MORTON, B. 2007. The evolution of the watering pot shells (Bivalvia: Anomalodesmata: Clavagellidae and Penicillidae). *Records of the Western Australian Museum* **24**(1), 19–64.

MORTON, B. & HARPER, E. M. 2001. Cementation in *Cleidothaerus albidus* (Lamarck, 1819) (Bivalvia: Anomalodesmata: Pandoroidea). *Molluscan Research* **21**, 1–15.

MORTON, J. E. 1958. The adaptations and relationships of the Xenophoridae (Mesogastropoda). *Proceedings of the Malacological Society of London* **33**(3), 89–100.

NAKAZIMA, M. 1967. Some observations on the soft parts of *Halicardia nipponensis* Okutani. *Venus* **25**(3–4), 147–158.

NARCHI, W. 1968. The functional morphology of *Lyonsia californica* Conrad, 1837 (Bivalvia). *Veliger* **10**, 305–313.

NARCHI, W. & DARIO, F. 2002. The anatomy and functional morphology of *Tivela ventricosa* (Gray, 1838) (Bivalvia: Veneridae). *Nautilus* **116**(1), 13–24.

NEVESSKAJA, L. A. 2009. Principles of systematics and the system of bivalves. *Paleontological Journal* **43**(1), 1–11.

NEVILL, A., BATE, S. & HOLDER, R. 2005. Modeling physiological and anthropometric variables known to vary with body size and other confounding variables. *Yearbook of Physical Anthropology* **48**, 141–153.

NEWELL, N. D. 1956. Primitive desmodont pelecypods of the Australian Permian. *American Museum Novitates* **1799**, 1–13.

Newell, N. D. 1965. Classification of the Bivalvia. *American Museum Novitates* **2206**, 1–25.

Newell, N. D. & Boyd, D. W. 1978. A palaeontologist's view of bivalve phylogeny. In C. M. Yonge & T. E. Thompson, editors, Evolutionary systematics of bivalve molluscs. *Philosophical Transactions of the Royal Society of London, Series B* **284**(1001), 203–214.

Newell, N. D., Cox, L. R., Keen, M., Rocque, A. L. & Smith, L. A. 1969*a*. Subclass Anomalodesmata Dall, 1889. In R. C. Moore, editor, *Treatise on invertebrate paleontology.* Part N. Mollusca 6, Bivalvia, volume 2, pages N818–N859. Geological Society of America and University of Kansas Press.

Newell, N. D., McCormick, L. & Moore, R. C. 1969*b*. Classification of Bivalvia. In R. C. Moore, editor, *Treatise on invertebrate paleontology.* Part N. Mollusca 6, Bivalvia, volume 1, pages N205–N224. Geological Society of America and University of Kansas Press.

Nicol, D. 1966. Descriptive ecology and geographic distribution of some Antarctic pelecypods. *Bulletins of American Paleontology* **51**(231), 1–102.

Nixon, K. C. 1999. The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* **15**(4), 407–414.

Nixon, K. C. 2002. *WinClada ver. 1.00.08.* Published by the author, Ithaca, NY, U.S.A.

Ockelmann, K. W. 1965. Development types in marine bivalves and their distribution along the Atlantic coast of Europe. *Proceedings of the European Malacological Congress* **1**, 25–35.

Odhner, N. H. J. 1917. Results of Dr. E. Mjöbergs Swedish scientific expeditions to Australia, 1910-1913. *Kungliga Svenska Vetenskapsakademiens handlingar* **52**(16), 1–115.

Ohno, T. 1996. Intra-periostracal calcified needles of the bivalve family Veneridae. *Bulletin de l'Institut Oceanographique Numero Special* **14**(4), 305–314.

Oliver, P. G. & Holmes, A. M. 2006. The Arcoidea (Mollusca: Bivalvia): A review of the current phenetic-based systematics. In R. Bieler, editor, Bivalvia — a look at the branches. *Zoological Journal of the Linnean Society* **148**(3), 237–251.

Owen, G. 1955. Observations on the stomach and digestive diverticula of the Lamellibranchia. I — the Anisomyaria and Eulamellibranchia. *Quarterly Journal of Microscopical Science* **96**(4), 517–537.

Owen, R. 1835. On the anatomy of *Clavagella*, Lam. *Transactions of the Zoological Society of London* **1**, 269–274.

Owen, R. 1842. On the anatomy of *Pholadomya candida. Proceedings of the Zoological Society of London* **10**, 150.

Owen, R. 1845. Editor's appendix etc. *Annals and Magazine of Natural History* **16**, 44–45.

Owen, R. 1855. *Lectures on the comparative anatomy and physiology of the invertebrate animals.* Longman, London, 2nd edition.

Packard, G. C. & Boardman, T. J. 2008. Model selection and logarithmic transformation in allometric analysis. *Physiological and Biochemical Zoology* **81**(4), 496–507.

Palazzi, S. & Villari, A. 2000. Mollusks and brachiopods from the submarine cave of Taormina, Sicily. *La Conchiglia, Supplement* **297**, 1–56.

Peck, L. S., Ansell, A. D., Webb, K. E., Hepburn, L. & Burrows, M. 2004. Movements and burrowing activity in the Antarctic bivalve molluscs *Laternula elliptica* and *Yoldia eightsi. Polar Biology* **27**(6), 357–367.

Peck, L. S., Brockington, S., Vanhove, S. & Beghyn, M. 1999. Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica. *Marine Ecology Progress Series* **186**, 1–8.

Peck, L. S., Powell, D. K. & Tyler, P. A. 2007. Very slow development in two Antarctic bivalve molluscs, the infaunal clam *Laternula elliptica* and the scallop *Adamussium colbecki*. *Marine Biology* **150**(6), 1191–1197.

Pelseneer, P. 1888*a*. Report on the anatomy of the deep-sea Mollusca collected by H.M.S. Challenger during the years 1873-1876. *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–76 under the Command of Captain George S. Nares and Captain Frank Tourle Thomson. Zoology* **27**, 1–42.

Pelseneer, P. 1888*b*. Les pélécypodes (ou lamellibranches) sans branchies. *Comptes Rendus Hébdomadaires des Séances de l'Académie des Sciences* **106**, 1029–1031.

Pelseneer, P. 1889. Les lamellibranches sans branchies. *Bulletin de la Société Zoologique de France* **14**, 111–113.

Pelseneer, P. 1891*a*. Contribution a l'etude des lamellibranches. *Archives de Biologie* **11**, 147–312.

Pelseneer, P. 1891*b*. Sur l'existence d'un groupe entier de lamellibranches hermaphrodites. *Zoologischer Anzeiger* **14**(353), 5–8.

Pelseneer, P. 1895. Hermaphroditism in Mollusca. *Quarterly Journal of Microscopical Science, New Series* **37**(145), 19–46.

Pelseneer, P. 1911. Les lamellibranches de l'expédition du Siboga. Partie anatomique. In M. Weber, editor, *Siboga-expeditie 34, monographie 53a*, 127 pages + 26 plates. Brill, Leiden.

Peterson, C. H. & Quammen, M. L. 1982. Siphon nipping: Its importance to small fishes and its impact on growth of the bivalve *Protothaca staminea* (Conrad). *Journal of Experimental Marine Biology and Ecology* **63**(3), 249–268.

de Pinna, M. C. C. 1991. Concepts and tests of homology in the cladistic paradigm. *Cladistics* **7**(4), 367–394.

Pojeta, Jr, J. 1971. Review of Ordovician pelecypods. *United States Geological Survey Professional Paper* **695**, 1–46.

Pojeta, Jr, J. 1978. The origin and early taxonomic diversification of pelecypods. In C. M. Yonge & T. E. Thompson, editors, Evolutionary systematics of bivalve molluscs. *Philosophical Transactions of the Royal Society of London, Series B* **284**(1001), 225–246.

Pojeta, Jr, J. 1986. Devonian rocks and Lower and Middle Devonian pelecypods of Guangxi, China, and the traverse group of Michigan. *United States Geological Survey Professional Paper* **1394A–G**.

Pojeta, Jr, J. & Gilbert-Tomlinson, J. 1977. Australian Ordovician pelecypod molluscs. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics* **174**, 1–64.

Pojeta, Jr, J. & Runnegar, B. N. 1985. The early evolution of diasome molluscs. In E. R. Trueman & M. N. Clarke, editors, *The Mollusca*, volume 10 (Evolution), pages 295–336. Academic Press, Orlando.

Pojeta, Jr, J. & Sohl, N. F. 1987. *Ascaulocardium armatum* (Morton, 1833), new genus (Late Cretaceous): The ultimate variation on the bivalve paradigm. *Memoirs of the Paleontological Society* **24**, 1–77.

Pojeta, Jr, J., Zhang, R. & Yang, Z. 1986. Chapter G: Systematic paleontology of Devonian pelecypods of Guangxi and Michigan. *United States Geological Survey Professional Paper* **1394**(G), 57–102.

Ponder, W. F. 1994. The anatomy and relationships of *Finella* and *Scaliola* (Caenogastropoda: Cerithioidea: Scaliolidae). In B. Morton, editor, *The malacofauna of Hong Kong and Southern China III: Proceedings of the Third International Workshop on the Malacofauna of Hong Kong and Southern China, Hong Kong, 13 April – 1 May 1992*, pages 215–241. Hong Kong University Press, Hong Kong.

Poutiers, J.-M. & Bernard, F. R. 1995. Carnivorous bivalve molluscs (Anomalodesmata) from the tropical Western Pacific Ocean, with a proposed classification and a catalogue of Recent species. In P. Bouchet, editor, Resultats des campagnes Musorstom, volume 14. *Mémoires du Muséum National d'Histoire Naturelle* **167**, 107–187.

Prendini, L. 2001. Species or supraspecific taxa as terminals in cladistic analysis? Groundplans versus exemplars revisited. *Systematic Biology* **50**(2), 290–300.

Prezant, R. S. 1979*a*. The structure and function of the radial mantle glands of *Lyonsia hyalina* (Bivalvia: Anomalodesmata). *Journal of Zoology* **187**(4), 505–516.

Prezant, R. S. 1979*b*. Shell spinules of the bivalve *Lyonsia hyalina*. *Nautilus* **93**(2-3), 93–95.

Prezant, R. S. 1981*a*. Taxonomic re-evaluation of the bivalve family Lyonsiidae. *Nautilus* **95**(2), 58–72.

Prezant, R. S. 1981*b*. The arenophilic radial mantle glands of the Lyonsiidae (Bivalvia: Anomalodesmata) with notes on lyonsiid evolution. *Malacologia* **20**(2), 267–289.

Prezant, R. S. 1981*c*. Comparative shell ultrastructure of lyonsiid bivalves. *Veliger* **23**, 289–299.

Prezant, R. S. 1984. Photoreceptors of the bivalve *Lyonsia hyalina*. *American Malacological Bulletin* **3**, 104.

Prezant, R. S. 1985*a*. Ontogenetic loss of arenophilic mantle glands in entodesmid bivalves. *American Zoologist* **25**(4), A129.

Prezant, R. S. 1985*b*. Derivations of arenophilic mantle glands in the Anomalodesmata. *Malacologia* **26**(1-2), 273–275.

Prezant, R. S. 1998*a*. Superfamily Pandoroidea. In P. L. Beesley, G. J. B. Ross & A. Wells, editors, *Mollusca: The southern synthesis. Fauna of Australia*, volume 5, Part A, pages 415–420. CSIRO Publishing, Melbourne.

Prezant, R. S. 1998*b*. Subclass Anomalodesmata. Introduction. In P. L. Beesley, G. J. B. Ross & A. Wells, editors, *Mollusca: The southern synthesis. Fauna of Australia*, volume 5, Part A, pages 397–405. CSIRO Publishing, Melbourne.

Prezant, R. S. 1998*c*. Superfamily Pholadomyoidea. In P. L. Beesley, G. J. B. Ross & A. Wells, editors, *Mollusca: The southern synthesis. Fauna of Australia*, volume 5, Part A, pages 405–407. CSIRO Publishing, Melbourne.

Prezant, R. S. 1998*d*. Class Bivalvia. Morphology and physiology (External features and shells). In P. L. Beesley, G. J. B. Ross & A. Wells, editors, *Mollusca: The southern synthesis. Fauna of Australia*, volume 5, Part A, pages 196–203. CSIRO Publishing, Melbourne.

Prezant, R. S. 1998*e*. Superfamily Verticordioidea. In P. L. Beesley, G. J. B. Ross & A. Wells, editors, *Mollusca: The southern synthesis. Fauna of Australia*, volume 5, Part A, pages 420–422. CSIRO Publishing, Melbourne.

Prezant, R. S. & Carriker, M. R. 1983. Functional microstructure of the lithodesma of *Mytilimeria nuttalli* (Bivalvia: Anomalodesmata). *Veliger* **25**(4), 326–328.

Prezant, R. S., Sutcharit, C., Chalermwat, K., Kakhai, N., Duangdeeand, T. & Dumrongrojwattana, P. 2008. Population study of *Laternula truncata* (Bivalvia: Anomalodesmata: Laternulidae) in the mangrove sand flat of Kungkrabaen Bay, Thailand with notes on *L.* cf. *corrugata*. In R. Bieler, K. Chalermwat, P. M. Mikkelsen, T. K. Siang & F. E. Wells, editors, Molluscs of Eastern Thailand: Proceedings of the International Marine Bivalve Workshop, Chantaburi, Thailand, August–September 2005, with contributions on other molluscan groups. *Raffles Bulletin of Zoology, Supplement* **18**, 57–73.

Prothero, J. 1986. Methodological aspects of scaling in biology. *Journal of Theoretical Biology* **118**(3), 259–286.

Purchon, R. D. 1956. The stomach in the Protobranchia and Septibranchia (Lamellibranchia). *Proceedings of the Zoological Society of London* **127**, 511–525.

Purchon, R. D. 1957. The stomach in the Filibranchia and Pseudolamellibranchia. *Proceedings of the Zoological Society of London* **129**, 27–60.

Purchon, R. D. 1958. The stomach in the Eulamellibranchia: Stomach type IV. *Proceedings of the Zoological Society of London* **131**, 487–525.

Purchon, R. D. 1959. Phylogenetic classification of the Lamellibranchia, with special reference to the Protobranchia. *Proceedings of the Malacological Society of London* **33**, 224–230.

Purchon, R. D. 1960*a*. Phylogeny in the Lamellibranchia. In R. D. Purchon, editor, *Proceedings of the Centenary and Bicentenary Congress of Biology, Singapore, December 2–9, 1958*, pages 69–82. University of Malaya Press, Singapore.

Purchon, R. D. 1960*b*. The stomach in the Eulamallibranchia; stomach types IV and V. *Proceedings of the Zoological Society of London* **135**, 431–489.

Purchon, R. D. 1963. Phylogenetic classification of the Bivalvia, with special reference to the Septibranchia. *Proceedings of the Malacological Society of London* **35**(23), 71–80.

Purchon, R. D. 1978. An analytical approach to a classification of the Bivalvia. In C. M. Yonge & T. E. Thompson, editors, Evolutionary systematics of bivalve molluscs. *Philosophical Transactions of the Royal Society of London, Series B* **284**(1001), 183–276.

Purchon, R. D. 1987. The stomach in the Bivalvia. *Philosophical Transactions of the Royal Society of London, Series B* **316**, 183–276.

Reeve, L. A. 1859. Monograph of the genus *Thracia*. In L. A. Reeve, editor, *Conchologia iconica; or, illustrations of the shells of molluscous animals*, volume 12, + 3 plates.

Reeve, L. A. 1872. Monograph of the genus *Clavagella*. In L. A. Reeve, editor, *Conchologia iconica; or, illustrations of the shells of molluscous animals*, volume 18.

Rehfeld, U. & Mehl, J. 1989. *Andinodesma radicostata* n. gen. n. sp., a grammysiid taxon from the Lower Devonian Catavi-Formation (Bolivia) and its autecological and phylogenetic implications. *Paläontologische Zeitschrift* **63**(3/4), 263–279.

Reid, R. G. B. 1965. The structure and function of the stomach in bivalve molluscs. *Journal of Zoology* **147**, 156–184.

Reid, R. G. B. & Crosby, S. P. 1980. The raptorial siphonal apparatus of the carnivorous septibranch *Cardiomya planetica* Dall (Mollusca: Bivalvia), with notes on feeding and digestion. *Canadian Journal of Zoology* **58**, 670–679.

Reid, R. G. B. & Reid, A. M. 1974. The carnivorous habit of members of the septibranch genus *Cuspidaria* (Mollusca: Bivalvia). *Sarsia* **56**, 47–56.

Ridewood, W. G. 1903. On the structure of the gills of the Lamellibranchia. *Philosophical Transactions of the Royal Society of London, Series B* **195**, 147–284.

Rieppel, O. & Kearney, M. 2002. Similarity. *Biological Journal of the Linnean Society* **75**(1), 59–82.

Rohr, D. M. 1993. Middle Ordovician carrier shell *Lytospira* (Mollusca, Gastropoda) from Alaska. *Journal of Paleontology* **67**(6), 959–962.

Roopnarine, P. D. 1996. Systematics, biogeography and extinction of chionine bivalves (Bivalvia: Veneridae) in tropical America: Early Oligocene–Recent. *Malacologia* **38**(1-2), 103–142.

Ruark, G. A., Martin, G. L. & Bockheim, J. G. 1987. Comparison of constant and variable allometric ratios for estimating *Populus tremuloides* biomass. *Forest Science* **33**, 294–300.

Runnegar, B. N. 1965. The bivalves *Megadesmus* Sowerby and *Astartila* Dana from the Permian of Eastern Australia. *Journal of the Geological Society of Australia* **12**(2), 227–252.

Runnegar, B. N. 1966. Systematics and biology of some desmodont bivalves from the Australian Permian. *Journal of the Geological Society of Australia* **13**(2), 373–386.

Runnegar, B. N. 1967. Desmodont bivalves from the Permian of Eastern Australia. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics* **96**, 1–108.

Runnegar, B. N. 1968. Preserved ligaments in Australian Permian bivalves. *Palaeontology* **11**, 94–103.

Runnegar, B. N. 1972. Anatomy of *Pholadomya candida* (Bivalvia) and the origin of the Pholadomyidae. *Proceedings of the Malacological Society of London* **40**, 45–58.

Runnegar, B. N. 1974. Evolutionary history of the bivalve subclass Anomalodesmata. *Journal of Paleontology* **48**(5), 904–939.

Runnegar, B. N. 1979. *Pholadomya candida* Sowerby: The last cadaver unearthed. *Veliger* **22**, 171–172.

Runnegar, B. N. & Newell, N. D. 1971. Caspian-like relict molluscan fauna in the South American Permian. *Bulletin of the American Museum of Natural History* **146**, 1–66.

Runnegar, B. N. & Newell, N. D. 1974. *Edmondia* and the Edmondiacea: Shallow-burrowing Paleozoic pelecypods. *American Museum Novitates* **2533**, 1–19.

von Salvini-Plawen, L. & Haszprunar, G. 1982. On the affinities of Septibranchia (Bivalvia). *Veliger* **25**(1), 83–85.

von Salvini-Plawen, L. & Steiner, G. 1996. Synapomorphies and plesiomorphies in higher classification of Mollusca. In J. D. Taylor, editor, *Origin and evolutionary radiation of the Mollusca*, pages 77–87. Oxford University Press, Oxford.

Sánchez, T. M. 2005. New Bivalvia and Rostroconchia from the Early Ordovician (Late Tremadoc–Middle Arenig) of Northwestern Argentina. *Journal of Paleontology* **79**(3), 532–541.

Sánchez, T. M. 2006. Taxonomic position and phylogenetic relationships of the bivalve *Goniophorina* Isberg, 1934, and related genera from the Early Ordovician of Northwestern Argentina. *Ameghiniana* **43**(1), 113–122.

Sánchez, T. M. 2008. The early bivalve radiation in the Ordovician Gondwanan basins of Argentina. *Alcheringa: An Australasian Journal of Palaeontology* **32**(3), 223–246.

Sánchez, T. M. & Vaccari, N. E. 2003. Ucumariidae new family (Bivalvia, Anomalodesmata) and other bivalves from the Early Ordovician (Tremadocian) of Northwestern Argentina. *Ameghiniana* **40**(3), 415–424.

Sartori, A. F. & Ball, A. D. 2009. Morphology and postlarval development of the ligament of *Thracia phaseolina* (Bivalvia: Thraciidae), with a discussion of model choice in allometric studies. *Journal of Molluscan Studies* **75**, 295–304.

Sartori, A. F. & Domaneschi, O. 2005. The functional morphology of the Antarctic bivalve *Thracia meridionalis* Smith, 1885 (Anomalodesmata: Thraciidae). *Journal of Molluscan Studies* **71**, 199–210.

Sartori, A. F. & Harper, E. M. 2009. Sticky bivalves from the Mesozoic: Clues to the origin of the anomalodesmatan arenophilic system. *Lethaia*, doi: 10.1111/j.1502-3931.2009.00166.x.

Sartori, A. F., Passos, F. D. & Domaneschi, O. 2006. Arenophilic mantle glands in the Laternulidae (Bivalvia: Anomalodesmata) and their evolutionary significance. *Acta Zoologica* **87**, 265–272.

Sartori, A. F., Printrakoon, C., Mikkelsen, P. M. & Bieler, R. 2008. Siphonal structure in the Veneridae (Bivalvia: Heterodonta) with an assessment of its phylogenetic application and a review of venerids of the Gulf of Thailand. In R. Bieler, K. Chalermwat, P. M. Mikkelsen, T. K. Siang & F. E. Wells, editors, Molluscs of Eastern Thailand: Proceedings of the International Marine Bivalve Workshop, Chantaburi, Thailand, August–September 2005, with contributions on other molluscan groups. *Raffles Bulletin of Zoology, Supplement* **18**, 103–125.

Sasaki, T. & Leal, J. H. 2008. *Dilemma japonicum* new species (Bivalvia: Anomalodesmata: Poromyidae): A new record of the genus from the Northwest Pacific. *Nautilus* **122**(3), 166–170.

Sato-Okoshi, W. & Okoshi, K. 2008. Characteristics of shell microstructure and growth analysis of the Antarctic bivalve *Laternula elliptica* from Lützow-Holm Bay, Antarctica. *Polar Biology* **31**(2), 131–138.

Savazzi, E. 1982. Adaptations to tube dwelling in the Bivalvia. *Lethaia* **15**, 275–297.

Savazzi, E. 1990. Shell biomechanics in the bivalve *Laternula*. *Lethaia* **23**(1), 93–101.

Savazzi, E. 1999. Boring, nestling and tube-dwelling bivalves. In E. Savazzi, editor, *Functional morphology of the invertebrate skeleton*, pages 205–237. J. Wiley, Chichester.

Savazzi, E. 2000. Morphodynamics of *Bryopa* and the evolution of clavagellids. In E. M. Harper, J. D. Taylor & J. A. Crame, editors, The evolutionary biology of the Bivalvia. *Geological Society, London, Special Publications* **177**, 313–327.

Savazzi, E. 2005. The function and evolution of lateral asymmetry in boring endolithic bivalves. *Paleontological Research* **9**(2), 169–187.

Scacchi, A. D. 1836. *Catalogus conchyliorum regni Neapolitani quae usque adhuc reperit.* Filiatre-Sebetii, Neapoli.

Scarlato, O. A. & Starobogatov, Y. I. 1983. System of the bivalve molluscs of the superoder Septibranchia. In I. M. Likharev, editor, *Molluscs. Their systematics, ecology and distribution. Abstracts of communications. Seventh meeting on the investigation of molluscs*, pages 7–13. Nauka, Leningrad.

Schmidt-Nielsen, K. 1984. *Scaling: Why is animal size so important?* Cambridge University Press, Cambridge, UK.

Schneider, J. A. 1995. Phylogeny of the Cardiidae (Mollusca, Bivalvia): Protocardiinae, Laevicardiinae, Lahilliinae, Tulongocardiinae subfam. n. and Pleuriocardiinae subfam. n. *Zoologica Scripta* **24**(4), 321–346.

Schneider, J. A. 1998*a*. Phylogeny of the Cardiidae (Bivalvia): Phylogenetic relationships and morphological evolution within the subfamilies Clinocardiinae, Lymnocardiinae, Fraginae and Tridacninae. *Malacologia* **40**(1-2), 321–373.

Schneider, J. A. 1998*b*. Phylogeny of stem-group eucardiids (Bivalvia: Cardiidae) and the significance of the transitional fossil *Perucardia*. *Malacologia* **40**, 37–62.

Schneider, J. A. 2001. Bivalve systematics during the 20th Century. *Journal of Paleontology* **75**, 1119–1127.

Schneider, J. A. & Carter, J. G. 2001. Evolution and phylogenetic significance of cardioidean shell microstructure (Mollusca, Bivalvia). *Journal of Paleontology* **75**(3), 607–643.

Seilacher, A. 1984. Constructional morphology of bivalves: Evolutionary pathways in primary versus secondary soft-bottom dwellers. *Palaeontology* **27**(2), 207–237.

Sepkoski, Jr, J. J. 2002. A compendium of fossil marine animal genera. *Bulletin of American Paleontology* **363**, 1–560.

Simões, M. G., Marques, A. C., Mello, L. H. C. & Anelli, L. E. 1997. Phylogenetic analysis of the genera of the extinct family Megadesmidae (Pelecypoda, Anomalodesmata), with remarks on its paleoecology and taxonomy. *Journal of Comparative Biology* **2**(2), 75–90.

Simone, L. R. L. & Cunha, C. M. 2008. Revision of the genus *Spinosipella* (Bivalvia: Verticordiidae), with descriptions of two new species from Brazil. *Nautilus* **122**(2), 57–78.

Skelton, P. W. & Benton, M. J. 1993. Mollusca: Rostroconchia, Scaphopoda and Bivalvia. In M. J. Benton, editor, *The fossil record 2*, pages 237–263. Chapman and Hall, London.

Smith, B. J. 1971. A revision of the family Clavagellidae (Pelecypoda Mollusca) from Australia with descriptions of two new species. *Journal of the Malacological Society of Australia* **2**, 135–161.

Smith, B. J. 1976. Revision of the Recent species of the family Clavagellidae (Mollusca: Bivalvia). *Journal of the Malacological Society of Australia* **3**, 187–209.

Smith, B. J. 1998. Superfamily Clavagelloidea. In P. L. Beesley, G. J. B. Ross & A. Wells, editors, *Mollusca: The southern synthesis. Fauna of Australia*, volume 5, Part A, pages 412–415. CSIRO Publishing, Melbourne.

Smith, E. A. 1885. Report on the Lamellibranchiata collected by H.M.S. Challenger, during the years 1873-1876. *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–76 under the Command of Captain George S. Nares and Captain Frank Tourle Thomson. Zoology* **13**, 1–341.

Smith, E. A. 1910. Note on the very young stage of the genus *Humphreyia*. *Proceedings of the Malacological Society of London* **9**(1), 23–25.

Smith, L. A. 1962*a*. Historical zoogeographic study of the Clavagellacea. *Veliger* **5**, 15–19.

Smith, L. A. 1962*b*. Revision of the Clavagellacea. *Veliger* **4**(4), 167–174.

Smith, R. J. 1984. Allometric scaling in comparative biology: Problems of concept and method. *AJP — Regulatory, Integrative and Comparative Physiology* **246**(2), R152–160.

Soliman, G. N. 1971. On a new clavagellid bivalve from the Red Sea. *Proceedings of the Malacological Society of London* **39**, 389–397.

Soot-Ryen, T. 1955. A report on the family Mytilidae (Pelecypoda). *Allan Hancock Pacific Expeditions* **20**(1), 1–174.

Soot-Ryen, T. 1966. Revision of the pelecypods from the Michael Sars North Atlantic deep sea expedition of 1910, with notes on the family Verticordiidae and other interesting species. *Sarsia* **24**, 1–32.

Sowerby, I, G. B. 1823. *The genera of recent and fossil shells, for the use of students in conchology and geology*, volume 19. G. B. Sowerby I, London.

Stanley, S. M. 1969. Bivalve mollusk burrowing aided by discordant shell ornamentation. *Science* **166**(3905), 634–635.

Stanley, S. M. 1970. Relation of shell form to life habits in the Bivalvia (Mollusca). *Geological Society of America Memoir* **125**, 1–296.

Stanley, S. M. 1972. Functional morphology and evolution of byssally attached bivalve mollusks. *Journal of Paleontology* **46**(2), 165–212.

Stanley, S. M. 1975. Adaptive themes in the evolution of the Bivalvia (Mollusca). *Annual Review of Earth and Planetary Sciences* **3**(1), 361–385.

Starobogatov, Y. I. 1992. Morphological basis for the phylogeny and classification of the Bivalvia. *Ruthenica* **2**, 1–26.

Stasek, C. R. 1963*a*. Geometrical form and gnomonic growth in the bivalved Mollusca. *Journal of Morphology* **112**(3), 215–231.

Stasek, C. R. 1963*b*. Synopsis and discussion of the association of ctenidia and labial palps in the bivalved Mollusca. *Veliger* **6**(2), 91–97.

Steiner, G. & Hammer, S. 2000. Molecular phylogeny of Bivalvia (Mollusca) inferred from 18S rRNA sequences with particular reference to the Pteriomorphia. In E. M. Harper, J. D. Taylor & J. A. Crame, editors, The evolutionary biology of the Bivalvia. *Geological Society, London, Special Publications* **177**, 11–29.

Taylor, J. D. 1973. The structural evolution of the bivalve shell. *Palaeontology* **16**, 519–534.

Taylor, J. D., Glover, E., Peharda, M., Bigatti, G. & Ball, A. 2004. Extraordinary flexible shell sculpture: The structure and formation of calcified periostracal lamellae in *Lucina pensylvanica* (Bivalvia: Lucinidae). In R. Bieler & P. M. Mikkelsen, editors, Bivalve studies in the Florida Keys: Proceedings of the International Marine Bivalve Workshop, Long Key, Florida, July 2002. *Malacologia* **46**(2), 277–294.

Taylor, J. D., Glover, E. A. & Braithwaite, C. J. R. 1999. Bivalves with 'concrete overcoats': *Granicorium* and *Samarangia*. *Acta Zoologica* **80**(4), 285–300.

Taylor, J. D., Kennedy, W. J. & Hall, A. 1969. The shell structure and mineralogy of the Bivalvia. Introduction, Nuculacea–Trigonacea. *Bulletin of the British Museum (Natural History) Zoology, Supplement* **3**, 1–125.

Taylor, J. D., Kennedy, W. J. & Hall, A. 1973. The shell structure and mineralogy of the Bivalvia. II. Lucinacea–Clavagellacea. Conclusions. *Bulletin of the British Museum (Natural History) Zoology* **22**(9), 253–294.

Taylor, J. D., Williams, S. T., Glover, E. A. & Dyal, P. 2007. A molecular phylogeny of heterodont bivalves (Mollusca: Bivalvia: Heterodonta): New analyses of 18S and 28S rRNA genes. *Zoologica Scripta* **36**, 587–606.

Tëmkin, I. 2006. Morphological perspective on the classification and evolution of Recent Pterioidea (Mollusca: Bivalvia). In R. Bieler, editor, Bivalvia — a look at the branches. *Zoological Journal of the Linnean Society* **148**(3), 253–312.

Thomas, K. A. 1994. The functional morphology and biology of *Pandora filosa* (Carpenter, 1864) (Bivalvia: Anomalodesmata: Pandoracea). *Veliger* **37**(1), 23–29.

Thompson, W. D. 1942. *On Growth and Form*. Cambridge University Press, Cambridge, UK, 2nd edition.

Trueman, E. R. 1954. Observations on the mechanism of the opening of the valves of a burrowing lamellibranch, *Mya arenaria*. *Journal of Experimental Biology* **31**(2), 291–305.

Trueman, E. R. 1964. Adaptive morphology in paleoecological interpretation. In J. Imbrie & N. D. Newell, editors, *Approaches to paleoecology*, pages 45–74. Wiley, New York; London.

Trueman, E. R. 1966. The cardinal ligament of the Tellinacea. *Proceedings of the Malacological Society of London* **37**, 111–117.

Trueman, E. R. 1969. General features of Bivalvia. Ligament. In R. C. Moore, editor, *Treatise on invertebrate paleontology*. Part N. Mollusca 6, Bivalvia, volume 1, pages N58–N64. Geological Society of America and University of Kansas Press.

Urban, H. J. & Mercuri, G. 1998. Population dynamics of the bivalve *Laternula elliptica* from Potter Cove, King George Island, South Shetland Islands. *Antarctic Science* **10**(2), 153–160.

Vermeij, G. J. 1987. *Evolution and escalation: An ecological history of life*. Princeton University Press.

Vokes, H. E. 1964. Margaritariidae, new family (Pelecypoda) and description of two species. *Tulane Studies in Geology* **2**, 135–141.

Waller, T. R. 1978. Morphology, morphoclines and a new classification of the Pteriomorphia (Mollusca: Bivalvia). In C. M. Yonge & T. E. Thompson, editors, Evolutionary systematics of bivalve molluscs. *Philosophical Transactions of the Royal Society of London, Series B* **284**(1001), 345–365.

Waller, T. R. 1990. The evolution of ligament systems in the Bivalvia. In B. Morton, editor, *The Bivalvia: Proceedings of a memorial symposium in honour of Sir Charles Maurice Yonge (1899–1986) at the IXth International Malacological Congress, 1986, Edinburgh, Scotland, U.K.*, pages 49–71. Hong Kong University Press, Hong Kong.

Waller, T. R. 1998. Origin of the molluscan class Bivalvia and a phylogeny of major groups. In P. A. Johnston & J. W. Haggart, editors, *Bivalves: An eon of evolution: Paleobiological studies honoring Norman D. Newell*, pages 1–45. University of Calgary Press, Calgary.

Ward, J. P. & Peck, L. S. 1997. The coldwater marine aquarium at the British Antarctic Survey. *Aquarium Sciences and Conservation* **1**(1), 53–63.

Waterhouse, J. B. 1965. Generic diagnosis for some burrowing bivalves of the Australian Permian. *Malacologia* **2**, 367–380.

Waterhouse, J. B. 1966. On the validity of the Permian bivalve family Pachydomidae Fischer 1887. *Journal of the Geological Society of Australia* **13**(2), 543–559.

Waterhouse, J. B. 1969*a*. The relationship between the living genus *Pholadomya* Sowerby and Upper Palaeozoic pelecypods. *Lethaia* **2**, 99–119.

Waterhouse, J. B. 1969*b*. The Permian bivalve genera *Myonia*, *Megadesmus*, *Vacunella* and their allies, and their occurrence in New Zealand. *New Zealand Geological Survey Paleontological Bulletin* **41**, 1–141.

Webb, C. M. 1986. Post-larval development of the tellinacean bivalves *Abra alba*, *Tellina fabula* and *Donax vittatus* (Mollusca: Bivalvia), with reference to the late larva. *Journal of the Marine Biological Association of the United Kingdom* **66**(3), 749–762.

Wiederhold, M. L., Sheridan, C. E. & Smith, N. K. R. 1990. Function of molluscan statocysts. In R. E. Crick, editor, *Origin, evolution, and modern aspects of biomineralization in plants and animals*, pages 393–408. Plenum Press, New York.

Yonge, C. M. 1928. Structure and function of the organs of feeding and digestion in the septibranchs, *Cuspidaria* and *Poromya*. *Philosophical Transactions of the Royal Society of London, Series B* **216**, 221–263.

Yonge, C. M. 1937. The formation of siphonal openings by *Thracia pubescens*. *Proceedings of the Malacological Society of London* **22**, 337–338.

Yonge, C. M. 1948*a*. Formation of siphons in Lamellibranchia. *Nature* **161**, 198–199.

Yonge, C. M. 1948*b*. Cleansing mechanisms and the function of the fourth pallial aperture in *Spisula subtruncata* (da Costa) and *Lutraria lutraria* (L.). *Journal of the Marine Biological Association of the United Kingdom* **27**(3), 585–596.

Yonge, C. M. 1952. Structure and adaptation in *Entodesma saxicola* (Baird) and *Mytilimeria nuttalli* Conrad. *University of California Publications in Zoology* **55**(10), 439–450.

Yonge, C. M. 1957. Mantle fusion in the Lamellibranchia. *Publicazione della Stazione Zoologica di Napoli* **29**, 151–171.

Yonge, C. M. 1962. On the primitive significance of the byssus in the Bivalvia and its effects in evolution. *Journal of the Marine Biological Association of the United Kingdom* **42**(1), 113–125.

Yonge, C. M. 1969. Functional morphology and evolution within the Carditacea (Bivalvia). *Proceedings of the Malacological Society of London* **38**, 493–527.

Yonge, C. M. 1976. Primary and secondary ligaments with the lithodesma in the Lyonsiidae (Bivalvia: Pandoracea). *Journal of Molluscan Studies* **42**(3), 395–408.

Yonge, C. M. 1978. Significance of the ligament in the classification of the Bivalvia. In C. M. Yonge & T. E. Thompson, editors, Evolutionary systematics of bivalve molluscs. *Philosophical Transactions of the Royal Society of London, Series B* **284**(1001), 231–248.

Yonge, C. M. 1982. Mantle margins with a revision of siphonal types in the Bivalvia. *Journal of Molluscan Studies* **48**(1), 102–103.

Yonge, C. M. 1983. Symmetries and the role of the mantle margins in the bivalve Mollusca. *Malacological Review* **16**, 1–10.

Yonge, C. M. & Morton, B. 1980. Ligament and lithodesma in the Pandoracea and the Poromyacea with a discussion on the evolutionary history in the Anomalodesmata (Mollusca: Bivalvia). *Journal of Zoology* **191**(2), 263–292.

Zacherl, D. C., Paradis, G. & Lea, D. W. 2003. Barium and strontium uptake into larval protoconchs and statoliths of the marine neogastropod *Kelletia kelletii*. *Geochimica et Cosmochimica Acta* **67**(21), 4091–4099.

Appendix A

List of examined extant material

This appendix supplies collection data for Recent taxa mentioned the analytical chapters of this volume. All listed lots were examined under a dissecting microscope and, for those which were the focus of more detailed anatomical and/or ultrastructural analyses, the methods used are noted. Additional information may be available from the institutions that house these specimens, whose abbreviations are as follows:

AMS	Australian Museum, Sydney, Australia
BAS	British Antarctic Survey, Cambridge, U.K.
BMNH	Natural History Museum, London, U.K.
CENEMAR	Centro de Estudos Marinhos do Atlântico Sul, Porto Alegre, Brazil
FMNH	Field Museum of Natural History, Chicago, U.S.A.
LACM	Los Angeles Natural History Museum, Los Angeles, U.S.A.
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MZSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil
NMNZ	Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand
ZMUC	Zoological Museum of the University of Copenhagen, Copenhagen, Denmark

Anomalodesmata

Asthenothaerus maxwelli Marshall, 2002

Lots: (1) NMNZ M. 183057; Taurikura Bay, Whangarei Harbour May 1962; col. W. Ponder (1 specimen with preserved soft parts). Analysis: dissections, histological sections, SEM (whole mounts, fractures and etched sections).

Brechites vaginiferus (Lamarck, 1818)

Lots: (1) author's collection, unregistered; Dampier Archipelago, Western Australia; col. B. Morton; leg. E. M. Harper (1 broken crypt) Analysis: SEM (etched sections).

***Bryopa aperta* (G. B. Sowerby I , 1823)**

Lots: (1) BMNH, unregistered; Malta, Dr Mamo; identified in the original label as "Clavagilla mamoi Gray" (1 specimen with preserved soft parts).

***Cardiomya cleryana* (d'Orbigny, 1846)**

Lots: (1) CENEMAR, unregistered; off Uruguay; J. Tarasconi Collection; leg. Rubem Aguilera January–July 2006 (3 specimens with preserved soft parts). Analysis: dissections, SEM (whole mounts, fractures and etched sections); (2) CENEMAR, unregistered; Santos (SP) to São Francisco do Sul (SC), Brazil; shrimp net, 35–62m depth, vessel "Trovão" (fisherman "Nildinho", from Bombinhas, SC), in the digestive tract of *Astropecten* sp., July–August 2001; J. Tarasconi Collection (1 specimen with preserved soft parts). Analysis: histological sections, SEM (whole mounts).

***Dianadema multangularis* (Tate, 1887)**

Lots: (1) BMNH 1890.3.24.185–191; Adelaide; col. C. H. Wigram, Esq.

***Grippina californica* Dall, 1912**

Lots: (1) LACM 37-167; 137 m, San Jaime Bank, Gulf Coast, Baja California Sur, Mexico (22°15' N; 110°17' W); leg. R/V Velero III (AHF BS 2005), 3 Mar 1937. [37-167]. Analysis: SEM (whole mounts, fractures and etched sections).

***Humphreyia strangei* (A. Adams, 1852)**

Lots: (1) BMNH 1910.12.31.1; off Phillip Island, Western Port Bay, Victoria, Australia, 4 fathoms depth, 4 December 1905; col. C. Gabriel, Esq. (1 specimen with preserved soft parts).

***Hunkydora novozelandica* (Reeve, 1859)**

Lots: (1) NMNZ M. 183056. 2004030; west of Little Barrier Island, Hauraki Gulf (sand suction dredged for beach replenishment at Kohi Beach, Auckland); 100% Ethanol; col. P. Poortman 2004 (1 specimen with preserved soft parts). Analysis: dissections, histological sections, SEM (whole mounts, fractures and etched sections).

***Laternula boschasina* (Valenciennes in Reeve, 1864)**

Lots: (1) author's collection, unregistered; Sungei Buloh Wetland Reserve, Northern Singapore (1°27' N; 103°36' E), 19 October 2005; preserved in 100% ethanol; col. and leg. Simon Morley (3 specimens with soft parts preserved). Analysis: histological sections and SEM (whole mounts).

***Laternula elliptica* (King & Broderip, 1831)**

Lots: (1) author's collection, unregistered; Admiralty Bay, King George Island, Antarctica (62°04' S; 58°21' W), 5–20m depth, muddy substrata (5 specimens with soft parts preserved) Analysis: dissections, histological sections and SEM (whole mounts); (2) author's collection, unregistered; Hangar Cove, near British Antarctic Survey's Rothera Research Station, c. 4m depth, 15 March 2007; col. scuba divers; leg. Lloyd Peck (20 small specimens with soft parts preserved). Analysis: dissections, SEM (whole mounts);

***Laternula marilina* (Valenciennes in Reeve, 1864)**

Lots: (1) author's collection, unregistered; Moreton Bay, Australia (27°28' S; 153°25' E), sand with seagrass; col. and leg. John Taylor (2 specimens with soft parts preserved). Analysis: histological sections and SEM (whole mounts).

Laternula truncata (Lamarck, 1818)

Lots: (1) author's collection, unregistered; Kungkrabaen Bay, Thailand (12°35' N; 101°54' E), seaward fringe of mangrove mud; col. A. F. Sartori, P. M. Mikkelsen, R. Bieler and C. Printakoon; det. A F Sartori (4 specimens with soft parts preserved and several isolated valves). Analysis: histological sections and SEM (whole mounts, fractures and etched sections). (2) author's collection, unregistered; Sungei Buloh Wetland Reserve, Northern Singapore (1°27' N; 103°36' E), 19 October 2005; preserved in 100% ethanol; col. and leg. Simon Morley (3 specimens with soft parts preserved). Analysis: SEM (whole mounts).

Lyonsia floridana Conrad, 1849

Lots: (1) FMNH 195496/2; Bunch Beach, Florida; col. Stehr and Jones 1974 (1 broken and one whole shell). Analysis: SEM (fractures); (2) FMNH 288890; Florida, Monroe County, Sta. FK-023, Lake Surprise (SW quadrant), Key Largo, Upper Florida Keys, -1m depth, 7 March 1995; hand dredged, algae washings, wet coll., EtOH/EtOH > 70%EtOH; col. R. Bieler and P. M. Mikkelsen; det. Florida Keys Project (1 fragmented specimen with preserved soft parts). Analysis: dissections, SEM (whole mounts); (3) BMNH 20070071; Blind Pass, Sanibel Island, Florida; leg. J. D. Taylor & E. A. Glover 1998; Accession number 2398 (5 specimens with preserved soft parts). Analysis: dissections; (4) unregistered histological sections prepared by Prof. B. Morton; Blind Pass; Sanibel Island, Florida; col. J. D. Taylor and E. A. Glover 1998.

Lyonsia norwegica (Gmelin, 1791)

Lots: (1) BMNH 1911.10.26.50090-50109; Shetland 1867; Norman Collection (14 shells and 2 isolated valves). Analysis: SEM (whole mounts, fractures and etched sections); (2) BMNH; "Sarsia" cruise stn. no. 360A (49°35' N; 4°10' W), 13 June 1964, 687m (1 specimen with fragmented left valve and preserved soft parts); (3) BMNH 20070070; off Newbiqqin, Northumberland, 110m; leg., det. and pres. J. A. Allen (3 specimens with preserved soft parts). Analysis: dissections, histological sections.

Myadora brevis (G. B. Sowerby I, 1829)

Lots: (1) author's collection, unregistered; Moreton Bay, Australia, dredged; col. and leg. John Taylor (2 specimens with soft parts preserved). Analysis: dissections.

Parilimya maoria (Dell, 1963)

Lots: (1) NMNZ 30369, TAN0707/122. Challenger Plateau (1 specimen with soft parts preserved; shell broken). Analysis: dissections, SEM (whole mounts).

Parilimya neozelanica (Suter, 1914)

Lots: (1) NMNZ M. 183055. 2004030; West of Little Barrier Island, c. 50m, Hauraki Gulf (sand suction dredged for replenishment of Kohi Beach, Auckland), 2004; col. P. Poortman (1 damaged specimen with preserved soft parts). Analysis: dissections, histological sections, SEM (whole mounts, fractures and etched sections).

Parvithracia fragilissima Marshall, 2002

Lots: (1) NMNZ M. 155144; paratypes; off Kakurangi Point (80942), 24 April 1980, 41°00.6' S; 169°06.0' E, research vessel "Tangaroa" (4 specimens with preserved soft parts). Analysis: dissections, histological sections, SEM (whole mounts, fractures and etched sections).

Parvithracia suteri Finlay, 1927

Lots: (1) NMNZ M. 183054. 98093; Bauza Basin, Doubtful Sound entrance, Fiordland, 200m, July 1998, 45°16.80' S; 166°52.50' E, research vessel "Munida" (6 specimens with preserved soft parts). Analysis: dissections, histological sections, SEM (whole mounts, fractures and etched sections).

Pendaloma micans (Hedley, 1901)

Lots: (1) NMNZ 29931, TAN0705/58; Chatham Rise (1 specimen with soft parts preserved, lacking the shell). Analysis: dissections.

Periploma compressum d'Orbigny, 1846

Lots: (1) CENEMAR, unregistered; Bombinhas (SC), Brazil, shrimp net 5–10m depth, fishing boat "Universo", September–October 1995; J. Tarasconi Collection; col. Sr Cecílio (1 specimen with preserved soft parts). Analysis: dissections, histological sections; (2) MZSP 31378; Praia de Itaparica, I. Itaparica, Bahia, Brazil July 1999, in sand, low tide; col. C. Magenta (1 specimen with preserved soft parts). Analysis: SEM (whole mounts, fractures and etched sections); (3) MZSP 44061; Brazil; Fixa 19; det. 2004 (1 adult specimen and several juveniles with preserved soft parts). Analysis: dissections, SEM (whole mounts and fractures); (4) MZSP 44065; Brazil; Fixa 17; det. 2004 (several juveniles with preserved soft parts). Analysis: SEM (whole mounts and fractures).

Periploma ovatum d'Orbigny, 1846

Lots: (1) author's collection, unregistered; Brazil, number 1374; leg. O. Domaneschi (1 whole shell and 1 left valve). Analysis: SEM (whole mounts and etched sections).

Pholadomya candida G. B. Sowerby I, 1823

Lots: (1) BMNH 1952.5.10.8; Holotype; Tortola; Geol. Collection (1 whole shell); (2) BMNH 1969.266; West Indies; Cuming Collection (1 whole shell); (3) BMNH 1967688; Paleo. Neg. nos: 45441, 45442; St Thomas, West Indies; C. T. Trechmann Collection 2176 (1 right valve); (4) ZMUC, unregistered; Tortola; possibly collected by Dr Ravn and sent to King Christian VIII by Mrs Ekhardt[1] (1 shell, left valve broken); (5) ZMUC, unregistered; St. Thomas; collected by Dr Ravn and given to Hofman Bang, who donated it to the University Museum (Copenhagen) on 17 April 1848. The date 20 April 1839 appears on the original label and may refer to the date the specimen was collected or given to Mr Bang (1 pair of unmatched right and left valves); (6) ZMUC, unregistered; St. Thomas; sent to King Christian VIII by Mrs Ekhardt (thus collected before 1848, when Christian VIII died) (1 whole shell); (7) ZMUC, unregistered; West Indies (1 whole shell); (8) ZMUC, unregistered; St. Thomas; collected by Dr Ravn in 1835 (1 specimen with preserved soft parts; partly dissected and microtomized by Morton, 1980).

Poromya cf *antarctica* (Hedley, 1916)

Lots: (1) BMNH 20001084; RV Polarstern St. No. 48–194, 244m depth, Antarctica (71°14.1' S; 12°27.7' W), 16 February 1998; Leg., Pres. & Det. K. Linse, 2000 (3 shells).

Poromya granulata (Nyst & Westendorp, 1839)

Lots: (1) BMNH 52.1.20.37, 52.11.22.37; Crowlin Islands, Skye; R. M. Andrew, Esq.

[1] the original label includes the name of Mrs Ekhardt only and the location is given as Campeche (Mexico); the name of Dr Ravn appears in one of two labels added later by someone who corrected the locality in the original label.

***Poromya tornata* (Jeffreys, 1876)**

Lots: (1) MNHN, unregistered; INCAL expedition, RV Jean Charcot Stn OS05, 4296m depth, Porcupine Abyssal Plain (47°31' N; 9°35' W), 7 August 1976; Det. J. Allen, 2005.

***Spheniopsis frankbernardi* Coan, 1990**

Lots: (1) LACM, unregistered. 222-271 m, sand, NW slope Santa Cruz Basin, 22 km SSW of Gull Id., Santa Cruz Id., California Channel Ids., California (33°46.1' N; 119°51.2' W); leg. R/V Thomas G. Thompson (BLM 809), 10 Feb 1977. [77-235]. Analysis: SEM (whole mounts, fractures and etched sections).

***Thracia convexa* Wood, 1815**

Lots: (1) unregistered; ESB Stn 68; 150cm quantitative; sagde 28 July 2007; col. John Hartley (1 specimen with soft parts preserved in 100% ethanol). Analysis: dissections.

***Thracia meridionalis* Smith, 1885**

Lots: (1) author's collection, unregistered; Admiralty Bay, King George Island, South Shetlands, Antarctica, February 1998; XVI Operação Antártica Brasileira; col. O. Domaneschi; Analysis: dissections, SEM (whole mounts and etched sections); (2) author's collection, unregistered; Admiralty Bay, King George Island, South Shetlands, Antarctica, March 2001; XIX Operação Antártica Brasileira; preserved in Bouin's fluid, transferred to 70% ethanol; col. F. D. Passos; Analysis: dissections, SEM (whole mounts).

***Thracia phaseolina* (Lamarck, 1818)**

Lots: (1) author's collection, unregistered; Ría de Ferrol, Galícia, Spain, van Veen grab, fine sand, 6m depth, 9 August and 20 August 2007; col. and leg. J. M. da Rocha (96 specimens with preserved soft parts, 10 of which with the shell broken). Analysis: dissections, confocal microscopy, SEM (whole mounts, fractures and etched sections). (2) author's collection, unregistered; Mill Bay, Kingsbridge Estuary, Devonshire, U.K. (National Grid Reference SX 74 2 38 2; 50°13'30" N; 4°45'55" W), intertidal region of a 0.33m spring tide, in sand with patches of eel seagrass *Zostera*; col. A. F. Sartori and E. M. Harper (6 specimens with preserved soft parts, 4 of which with the shell broken). Analysis: dissections, confocal microscopy, SEM (whole mounts and fractures)

***Thracia similis* Couthouy, 1839**

Lots: (1) MZSP 19.972; Saco da Ribeira, Ubatuba, São Paulo, Brazil; col. P. Mowtouchet 1967; det. A. F. Sartori 2004 (several shells and isolated valves) Analysis: SEM (etched sections); (2) MZSP 19.986; Baía da Ilha Grande, Angra dos Reis, Rio de Janeiro, Brazil, "W. Besnard" station 359, 11m depth, March 1969; det. A. F. Sartori 2004 (17 specimens with soft parts preserved). Analysis: SEM (whole mounts).

***Thracidora arenosa* (Hedley, 1904)**

Lots: (1) AMS C447895; 003159B TAS; West of Sandy Cape (41°29.500' S; 144°24.400' E), 119m, MT "Springhtly", 15 April 1973, Stn: S73–2122; pres. BMR; det. I. Loch 2005 (1 whole shell). Analysis: SEM (whole mounts, fractures and etched sections).

***Thraciopsis angustata* (Angas, 1867)**

Lots: (1) author's collection, unregistered; seaward side of N. Stradbroke Island, Moreton Bay, Queensland, Australia (27°24.03' S; 153°29.37' E), dredged 11m, in sand with *Syringodium*,

February 2005; preserved in 100% ethanol; col. and leg. E. A. Glover and J. D. Taylor (1 specimen with preserved soft parts). Analysis: dissections, histological sections, SEM (whole mounts, fractures and etched sections).

***Thraciopsis subrecta* Cotton & Godfrey, 1938**

Lots: (1) BMNH 20040007; near Rottnest Island, Perth, Western Australia, dredge stn 18, depth 26m, January 1996; col. and leg. J. D. Taylor and E. A. Glover; accession no. 2388 (1 left valve). Analysis: SEM (whole mounts and fractures).

***Trigonothracia jinxingae* (Xu, 1980)**

Lots: (1) author's collection, unregistered; Xiamen Harbour, Fujian Province, China, January 1994; col. B. Morton; leg. E. M. Harper. Analysis: SEM (whole mounts and etched sections). (2) unregistered histological sections prepared by Prof. B. Morton; Xiamen Harbour, Fujian Province, China; col. B. Morton January 1994.

Outgroups

***Anodonta anatina* (Linnaeus, 1758)**

Lots: (1) author's collection, unregistered; Thames and Kennet Marina, Caversham, U.K. (51°27'42" N; 0°56'59" W), depth ∘1.5m, July 2007; col. A. Zieritz and A. F. Sartori; det. A. Zieritz. Analysis: dissections

***Tellina fabula* Gmelin, 1791**

Lots: (1) author's collection, unregistered; Mill Bay, Kingsbridge Estuary, Devonshire, U.K. (National Grid Reference SX 74 2 38 2; 50°13'30" N; 4°45'55" W), intertidal region of a 0.33m spring tide, in sand with patches of eel seagrass *Zostera*; col. A. F. Sartori and E. M. Harper. Analysis: dissections

Appendix B

Assumptions and properties of the simple and full allometric equations

The two-parameters power function $y = bx^a$, proposed by Huxley (1932) as the "equation of simple allometry", has been by far the most widely used mathematical model in allometric studies. It is generally applied to log-transformed empirical data (in the form $\ln y = \ln b + a \ln x$) and its success is largely due to its simplicity, applicability to a great number of cases, and straightforward biological interpretation (Gould, 1966, 1971). However, a critical assumption of this equation is that the relationship between the studied variables passes through the origin (Albrecht *et al.*, 1993; Packard & Boardman, 2008), a condition that is only strictly satisfied for morphological data when the traits being compared begin their ontogenetic trajectories simultaneously (Huxley, 1932). In the common case where y represents a dimension of an organ or structure of interest and x is a measure of total body size, the assumption of a zero intercept will be very rarely met because organs differentiate at distinct body sizes in the ontogeny of virtually all organisms (Thompson, 1942). This limitation of the simple allometric equation was recognised by Huxley (1932, p. 241), who proposed a distinct mathematical model to account for differences in the time of onset of growth of trait y and standard x, and recommended it "should be taken as the theoretical basis for analysis". The formula consisted of the simple allometric equation modified by addition of an intercept, yielding the three-parameters power function $y = bx^a + c$, later termed full allometric model by Albrecht & Gelvin (1987) and Albrecht *et al.* (1993).

In practice, a non-zero intercept (parameter c) will be usually negligible because allometric relationships are generally determined for a range of body sizes that is far departed from the first stages of ontogeny, when the differentiation of most organs takes place (Huxley, 1932). Nevertheless, whenever the body size (or other standard) at which the organ of interest arises is included in the studied range or is relatively near to the limits of this range, the simple allometric equation will render an inappropriate description of the data. This was clearly shown by an interesting discussion on horn evolution in brontotheriids (Mammalia) by Bales (1996). After fitting a three-power function to a bivariate plot of horn length versus skull length in adults of Eocene and Oligocene species, Bales (1996) showed how standard allometric analysis using the two-parameters power function on a logarithmic morphospace had led previous investigators to conclusions that were not supported by the original data.

Despite the apparent advantages of the three-parameters power function in these and similar examples, its application has been uncommon and controversial. Klingenberg (1998) criticised its use not only because it cannot be derived from theoretical principles of multiplicative growth, but also because a nonzero intercept may lead to unrealistic predictions of the dimensions of trait y, a point also made by Nevill *et al.* (2005). The equation of simple allometry was proposed as a true biological law by Huxley (1932) on the assumption that the rate of growth of an organ is proportional to its size, hence reflecting the fundamental nature of growth as a process of self-multiplication. However, subsequent authors have denied any special significance to the equation, other than its empirical value in describing a wide range of allometric relationships (Thompson, 1942; Gould, 1966; Prothero, 1986; LaBarbera, 1989, among others).

Commenting on the issue of the intercept, Klingenberg (1998, p. 106) specifically referred to Bales' study (1996) and remarked that the latter author "considers it unrealistic that the line of simple allometry must always pass through the origin (for untransformed data), but seems to have no such objections against the negative y intercept of this [sic] fitted line that implies negative horn lengths in brontotheres!". I agree that in the treatment of numerous variables the assumption of a zero intercept may be fully justified. For instance, in a study of oxygen consumption relative to body size a zero intercept could be the natural outcome of the fact that metabolism of an animal arises simultaneously with the animal itself. However, in the specific case of morphological traits of late ontogenetic appearance, a negative y intercept need not be interpreted as the size of the trait at zero body size, a biological impossibility. Instead, it corresponds to a positive x intercept (x_0), which provides an estimate of the size attained by the body (or other standard) before the onset of growth of the structure of interest. The estimate is calculated by substituting the variable y for zero in the full

allometric model and then solving for x, which gives $x_0 = (-c/b)^{1/a}$. For the parivincular ligament of *T. phaseolina* (discussed in chapter 2), the value of shell length thus arrived at is 2.61 mm and the negative values of ligament length obtained by extrapolation of the curve of best fit to smaller shell lengths are just an indication that the ligament has not yet differentiated at those body sizes. Similarly, the curve of best-fit obtained by Bales (1996, p. 488) crossed the x-axis at approximately 400 mm, a value that was taken as an estimate of "the skull size reached by brontothere skulls before horn evolution began".

Finally, while the mathematical meaning of the exponents of the two- and three-parameters power functions is the same, i.e. when different from 1 they both indicate that the relationship between the variables departs from linearity (Albrecht *et al.*, 1993), their biological interpretation differs (Albrecht & Gelvin, 1987). The slope m of a curve describing the relationship between log-transformed dimensions of a trait y and a standard x is equivalent to the ratio of the relative growth-rates of these variables and indicates whether and in which direction the proportion between the two (the y/x ratio) is being altered (Huxley, 1932; Smith, 1984; Schmidt-Nielsen, 1984). Whenever $m = 1$, the relative size of the traits under consideration remains constant (isometry). When $m < 1$ trait y becomes relatively smaller (negative allometry) and when $m > 1$ it becomes relatively larger (positive allometry) as x increases. The two-parameters power function ($y = bx^a$) is represented by a straight line when log-transformed ($\ln y = \ln b + a \ln x$), meaning that its slope is constant and equivalent to the exponent ($m = a$). Log-transformation of the three-parameters power function ($y = bx^a + c$), however, yields a curvilinear relationship (Fig. B.1A) given by the equation $\ln y = \ln (bx^a + c)$, which may be rewritten as a function of $\ln x$:

$$\ln y = \ln (b\, e^{a \ln x} + c) \tag{B.1}$$

The shifting slope of the curve is then calculated by differentiating equation (B.1) with respect to $\ln x$, which results in the expression:

$$m = a\, b\, e^{a \ln x} / (c + b\, e^{a \ln x}) \tag{B.2}$$

Equation (B.2) shows that: (1) m is equivalent to the exponent a if, and only if, the intercept c is zero, which simplifies full into simple allometric model; (2) in every other case, m approaches the value of exponent a as x increases because the limit of $(b\, e^{a \ln x})/(c + b\, e^{a \ln x})$ as x approaches positive infinity is 1. However, the larger the modulus of intercept c, the larger x must be before m becomes asymptotic with a

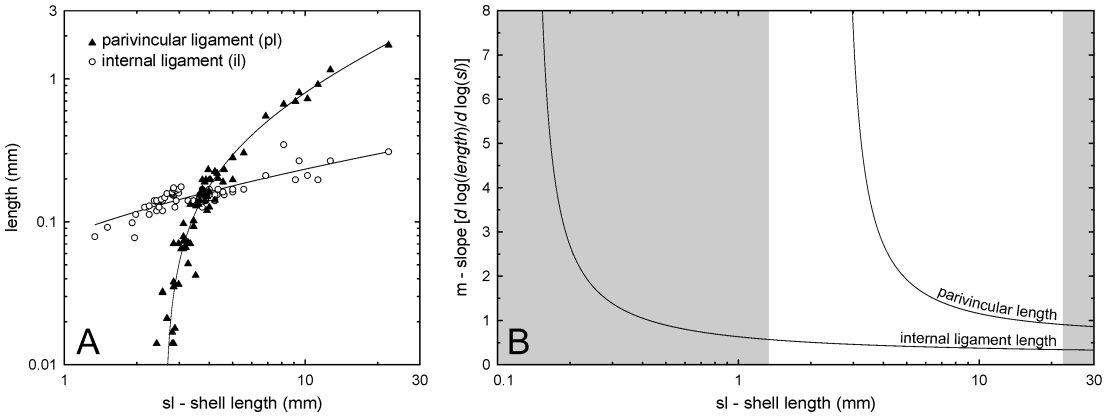


Figure B.1: *T. phaseolina*. **A**. Observed values of lengths of the internal (*il*, ○) and parivincular (*pl*, ▲) ligaments plotted against shell length (sl) in a log-log scale. Curves of best fit obtained by the three-parameters power function on a linear scale were algebraically transformed to apply to logarithms and added to the graph. **B**. Slope of the curves shown in **A** plotted against shell length in a log-linear scale. The area of the graph in grey represent predicted slopes for shell lengths that were not observed.

(Fig. B.1B). Thus, the exponent of the full allometric model indicates the value assumed by the ratio of the relative growth rates of y and x after increase of the variables has rendered the influence of a distinct onset of growth negligible; (3) if $c < 0$, the value of m approaches positive infinity as x decreases toward x_o (Fig. B.1B). This is because substitution of $\ln x$ for $\ln x_0 = [\ln(-c/b)]/a$ makes the denominator of the function equal to zero. As x increases toward x_0, m approaches negative infinity but this result is futile because, as previously discussed, trait y does not exist when $x \leqslant x_0$; (4) if $c > 0$, $m = 0$ when $x = 0$. This could be interpreted as evidence that the standard x arises previous to y during ontogeny.

Figure B.1 illustrates these properties for the relationships of lengths of the internal and parivincular ligaments against shell length of *T. phaseolina*, described in section 2.3.1.3. The estimated onset of growth of the internal ligament is relatively distant from the range of shell lengths represented in my sample (Fig. B.1B). For this reason, by the lower limit of the observed range of body sizes m has approached the value of the exponent a closely enough that the relationship between *il* and *sl* may be described equally well by a model assuming a constant slope, such as the two-parameters power function. In this case, the latter model may be selected for simplicity in spite of the probably wrong assumption of a zero intercept, as previously discussed. For the parivincular ligament dataset (Fig. B.1A), however, the model of choice must allow for a curvilinear relationship of log-transformed variables, a condition that is fulfilled by many distinct formulae (see Ruark *et al.*, 1987; Feener *et al.*, 1988; Bervian *et al.*, 2006; Lagergren *et al.*, 2007, for a few examples). However, while all these models allow slope

m to vary and may provide a good fit to the data, they generally introduce a number of non-interpretable parameters to the analysis. The full allometric equation, on the contrary, is a simple expression that may be successfully applied to instances in which a curvilinear relationship on logarithmic plots results from a non-zero intercept that is biologically justifiable. In the common case in which the allometry of a structure of late ontogenetic appearance is considered, a non-zero intercept will provide an estimate of the size attained by the body or other standard previously to the onset of growth of the structure of interest.

Appendix C

Character definitions

Formal definitions of the characters and their states used to construct the data matrix reproduced in Table 5.2 are given below. For each character, values of the consistency index (CI), retention index (RI) and optimisation details are given based on the strict consensus tree given in Figure 5.4, produced by analysis of the dataset with *Thracidora arenosa*, *Grippina californica* and *Spheniopsis frankbernardi* excluded. The section and page numbers of this volume in which a discussion of each character may be found are also indicated for convenience.

General shell morphology

1. Umbonal slit: absent (0); present (1). CI=0.5; RI=0.8; section 4.2.4, page 102.

Unambiguous: Laternulidae (0→1), Periplomatidae (0→1).

2. Crypt: absent (0); present (1). CI=1; RI=1; section 4.2.5, page 104.

Unambiguous: Clavagelloidea (0→1).

3. Crypt is secreted by: left mantle lobe only (0); both mantle lobes (1). CI=1; RI=1; section 4.2.5, page 104.

Coded only in taxa possessing a crypt.

Unambiguous: Clavagellidae (1→0).

4. Ability to cement the valves to a hard substratum: absent (0); present, via the right valve (1); present, via the left valve (2). CI=0.66; RI=0.5; section 4.2.6, page 105.

Unambiguous: *Clavagella australis* (0→2), Cleidothaeridae (0→1), *Myochama anomioides* (0→1).

5. Calcified periostracal sculpture: absent (0); present in the form of granules or spikes (1); present, resembling bricks or paving stones (2). CI=0.28; RI=0.5; section 4.2.2, page 97.

Unambiguous: Clade C (0→1), *Laternula elliptica* (1→0), *Cardiomya cleryana* (1→0), *Pendaloma micans* (1→0), *Hunkydora novozelandica* (1→2), *Thraciopsis angustata* (1→2). *Asthenothaerus maxwelli* (1→2).

6. Size of calcified periostracal elements: virtually uniform throughout the dissoconch (0); coarser posterior to the diagonal ridge (1); absent or fading posterior to the diagonal ridge (2). CI=0.66; RI=0.85; section 4.2.2, page 97.

Coded only in taxa possessing calcified periostracal elements.

Unambiguous: Clade H (0→2), Clade I (0→1).

ACCTRAN: *Myadora brevis* + *Myochama anomioides* (1→0).

DELTRAN: *Myadora brevis* (1→0).

7. Calcified periostracal sculpture organised in radial lines: absent (0); present (1). CI=1; RI=1; section 4.2.2, page 97.

Coded only in taxa possessing calcified periostracal elements.

Unambiguous: Clade K (1→0).

8. Discontinuous (dotted) pallial line: absent (0); present (1). CI=1; RI=1; section 4.3.4, page 108.

Unambiguous: Pandoridae (0→1).

HINGE

9. Disjunct ontogeny of fibrous ligament: absent (F1 is retained as the sole adult ligament) (0); present, with F2 supported by nymphal ridges (1); present, with F2 supported by chondrophores (2). CI=0.25; RI=0.5; section 2.4.1, page 37.

Unambiguous: Laternulidae (0→2), *Poromya granulata* (0→1), *Thracia meridionalis* (0→1), Periplomatidae (0→2), *Trigonothracia jinxingae* (0→2).

ACCTRAN: Palaeoheterodonta (0→1), Tellinoidea (0→1), Pholadomyoidea (0→1).

DELTRAN: Palaeoheterodonta (0→1), Tellinoidea (0→1), Pholadomyoidea (0→1).

10. F1 extensively calcified medially, forming a solid ossicle (lithodesma): absent (0); present (1). CI=0.33; RI=0.77; section 2.4.1, page 37.

Unambiguous: *Pandora filosa* + *Pandora gouldiana* (0→1), Clade E (0→1), Clavagellidae (1→0).

11. Anterior lateral tooth on the right valve: absent (0); present (1). CI=0.5; RI=0.83; section 4.2.3, page 100.

Unambiguous: Archiheterodonta + Tellinoidea (0→1), Clade N (0→1).

12. Posterior lateral tooth on right valve: absent (0); present (1). CI=0.25; RI=0.62; section 4.2.3, page 100.

Unambiguous: Archiheterodonta + Tellinoidea (0→1), *Cardiomya cleryana* (0→1), *Hunkydora novozelandica* (0→1), Clade N (0→1).

13. Cardinal tooth on right valve: absent (0); present (1). CI=0.25; RI=0.4; section 4.2.3, page 100.

Unambiguous: Anomalodesmata (1→0).

ACCTRAN: *Euciroa pacifica* + *Verticordia triangularis* + *Lyonsiella formosa* + *Poromya granulata* + *Cardiomya cleryana* (0→1), *Lyonsiella formosa* (1→0), *Cardiomya cleryana* (1→0).

DELTRAN: *Euciroa pacifica* (0→1), *Verticordia triangularis* (0→1), *Poromya granulata* (0→1).

14. Cardinal tooth on left valve: absent (0); present (1). CI=0.5; RI=0.75; section 4.2.3, page 100.

Unambiguous: Anomalodesmata (1→0), Cleidothaeridae (0→1).

15. Crura: absent (0); present (1). CI=1; RI=1; section 4.2.3, page 100.

Unambiguous: Pandoridae (0→1).

Shell microstructure

16. Microstructure of the middle shell layer: crossed-lamellar (0); nacreous (1); fine-grained (2). CI=0.28; RI=0.16; section 4.2.1, page 92.

Unambiguous: Archiheterodonta + Tellinoidea (1→0), *Cardiomya cleryana* (1→2), *Trigonothracia jinxingae* (1→2), *Thracia meridionalis* (1→2), *Asthenothaerus maxwelli* (1→2), *Parvithracia fragilissima* (1→2), *Parvithracia suteri* (1→2).

17. Microstructure of the inner shell layer: complex crossed-lamellar (0); nacreous (1); fine-grained (2). CI=0.33; RI=0.55; section 4.2.1, page 92.

Unambiguous: Archiheterodonta + Tellinoidea (1→0), Clade K (1→2), *Pendaloma micans* + *Offadesma angasi* (2→1), *Myadora brevis* + *Myochama anomioides* (2→1), *Cardiomya cleryana* (1→2).

Acctran: Cleidothaeridae (2→1).

Deltran: *Cleidothaerus albidus* (2→1).

Mantle

18. Ventral mantle fusion separating pedal and posterior inhalant apertures: absent (0); present, not involving left and right periostracal grooves (1); present, involving periostracal grooves (ventral margin covered by a continuous periostracal sheet) (2). CI=0.66; RI=0.75; section 4.3.1, page 105.

Unambiguous: Clavagelloidea (1→2).

Acctran: Heterodonta (0→1), Archiheterodonta (1→0).

Deltran: Anomalodesmata (0→1), Tellinoidea (0→1).

19. Fused mantle margins form a wide band ventrally: absent (0); present (1). CI=0.5; RI=0.66; section 4.3.1, page 105.

Coded as inapplicable in taxa lacking ventral fusion of the mantle margins.

Unambiguous: Pholadomyoidea (0→1), *Offadesma angasi* (0→1).

20. Orbital muscles: absent (0); present (1). CI=0.33; RI=0.6; section 4.3.4, page 108.

Unambiguous: *Pholadomya candida* (0→1), Laternulidae (0→1).

Acctran: Periplomatidae (0→1).

Deltran: *Periploma compressum* + *Pendaloma micans* + *Offadesma angasi* (0→1).

21. Fourth pallial aperture: absent (0); present (1). CI=0.16; RI=0.72; section 4.3.1, page 105.

Unambiguous: Clade C (0→1), Laternulidae (1→0), *Humphreyia strangei* + Clavagellidae (1→0), *Euciroa pacifica* + *Verticordia triangularis* + *Lyonsiella formosa* + *Poromya granulata* + *Cardiomya cleryana* (1→0), *Cochlodesma praetenue* (1→0), *Myadora brevis* (1→0).

22. Arenophilic glands: absent (0); present (1). CI=0.2; RI=0.73; section 3.2.3.2, page 76.

Unambiguous: *Pendaloma micans* + *Offadesma angasi* (0→1), *Verticordia triangularis* (0→1).

ACCTRAN: Clade C (0→1), Clade I (1→0), *Bentholyonsia teramachii* (0→1).

DELTRAN: Pholadomyoidea (0→1), Clade F (0→1), *Bentholyonsia teramachii* (0→1).

23. Glandular area on the internal epithelium of the right mantle lobe, marked by tall, columnar cells with eosinophilic secretory globules: absent (0); present (1). CI=0.33; RI=0.83; section 4.3.3, page 108.

Unambiguous: Clade K (0→1), *Cleidothaerus maxwelli* (1→0), *Myochama anomioides* (1→0).

24. Pigmentation of the pallial tissue (mantle, siphons or both): absent (0); present (1). CI=0.2; RI=0.69; section 4.3.2, page 107.

Unambiguous: Tellinoidea (1→0), Clade I (1→0), *Poromya granulata* (0→1) Cleidothaeridae (0→1).

ACCTRAN: Parilimyidae (1→0).

DELTRAN: *Parilimya neozelanica* (1→0).

SIPHONS

25. External walls of the siphons covered in periostracum: absent (0); present (1). CI=1; RI=1; section 4.3.1, page 105.

Coded as inapplicable in taxa with siphons shorter than the combined width of their inhalant and exhalant apertures (in preserved specimens), because in these cases the siphonal walls could not be confidently distinguished from the surrounding mantle margins.

Unambiguous: Clade F (0→1).

26. Tentacles bordering inhalant and exhalant apertures: absent or represented by papillae lacking an apical ciliated pit (0); present, tipically organized in multiple rows and bearing an apical ciliated pit (1). CI=0.25; RI=0.8; section 4.3.8, page 110.

Unambiguous: *Frenamya ceylanica* + *Pandora filosa* + *Pandora gouldiana* (0→1), Clade F (0→1), *Euciroa pacifica* + *Verticordia triangularis* + *Lyonsiella formosa* + *Poromya granulata* + *Cardiomya cleryana* (0→1).

ACCTRAN: Palaeoheterodonta (0→1).

DELTRAN: Palaeoheterodonta (0→1).

27. Siphonal eyes: absent (0); present (1). CI=1; RI=1; section 4.3.8, page 110.

Unambiguous: Laternulidae (0→1).

28. Siphonal cowl: absent (0); present (1). CI=0.5; RI=0; section 4.3.9, page 112.

Unambiguous: *Lyonsiella formosa* (0→1), *Poromya granulata* (0→1).

29. Hypertrophied siphonal retractors (taenioid muscles): absent (0); present and inserted among "normal" siphonal retractors (1); present, with a separate insertion on the shell wall (2). CI=0.33; RI=0.55; section 4.3.5, page 108.

Unambiguous: Pholadomyoidea (0→1), Parilimyidae (1→2), *Bentholyonsia teramachii* (0→1→2), *Lyonsiella formosa* (0→1→2).

30. Siphonal tubes forming mucus lined passages through the sediment: absent (0); present (1). CI=0.5; RI=0.5; section 4.3.7, page 110.

Unambiguous: Periplomatidae (0→1), *Thracia meridionalis* (0→1).

31. Central layer of circular musculature in the siphonal walls: absent (0); present (1). CI=0.5; RI=0.87; section 4.3.6, page 110.

Coded as inapplicable in taxa lacking siphons.

Unambiguous: Clade I (1→0), Parilimyidae (1→0).

32. Position of the siphonal nerves: embeded in the first longitudinal muscle layer internal to the hemocoel (0); embeded in the hemocoel (1). CI=0.5; RI=0.85; section 4.3.6, page 110.

Coded as inapplicable in taxa lacking siphons.

Unambiguous: Clade I (0→1).
ACCTRAN: *Pendaloma micans* + *Offadesma angasi* (1→0).
DELTRAN: *Offadesma angasi* (1→0).

GILLS

33. Nature of the gills: ctenidia (0); septum (1). CI=0.5; RI=0; section 4.4.1, page 112.

Unambiguous: *Poromya granulata* (0→1), *Cardiomya cleryana* (0→1).

34. Alignment of the gills: approximately parallel to the mid sagittal plane of the body (0); approximately perpendicular to the mid sagittal plane of the body (1). CI=1; RI=1; section 4.4.1, page 112.

Unambiguous: Septibranchia (0→1).

35. Ascending lamella of the outer demibranch: present (0); absent (1). CI=0.5; RI=0; section 4.4.1, page 112.

Coded as inapplicable in species lacking filamentous gills.

ACCTRAN: Heterodonta (0→1), Archiheterodonta (1→0).
DELTRAN: Anomalodesmata (0→1), Tellinoidea (0→1).

36. Plication of ctenidia: absent (0); present (1). CI=0.25; RI=0.62; section 4.4.2, page 115.

Coded as inapplicable in species lacking filamentous gills.

Unambiguous: Anomalodesmata (0→1), Septibranchia (1→0), *Pendaloma micans* (1→0), *Parvithracia suteri* (1→0).

37. Enlarged apical filaments: absent (0); present (1). CI=0.16; RI=0.37; section 4.4.2, page 115.

Coded as inapplicable in species lacking filamentous gills.

Unambiguous: *Pandora inaequivalvis* (0→1), *Pholadomya candida* (0→1), Clade H (0→1), *Offadesma angasi* (0→1), *Asthenothaerus maxwelli* (0→1).
ACCTRAN: Cleidothaeridae (0→1).
DELTRAN: *Cleidothaerus albidus* (0→1).

38. Marginal food groove in the inner demibranch: absent (0); present (1). CI=0.25; RI=0; section 4.4.5, page 117.

Coded as inapplicable in species lacking filamentous gills.

Unambiguous: Tellinoidea (1→0), *Parilimya* sp1 (1→0), *Bentholyonsia teramachii* (1→0), *Pendaloma micans* (1→0).

39. Paired tentacular projections on the border of the inter-siphonal septum: absent (0); present (1). CI=0.25; RI=0.25; section 4.4.3, page 115.

Unambiguous: *Hunkydora novozelandica* (0→1), *Thraciopsis angustata* (0→1).

ACCTRAN: Periplomatidae (0→1), *Myadora brevis* + *Myochama anomioides* (0→1).

DELTRAN: *Periploma compressum* + *Pendaloma micans* + *Offadesma angasi* (0→1), *Myadora brevis* (0→1).

40. Connection between gills and body wall: ciliary (0); cuticular (1); tecidual (2). CI=0.4; RI=0.62; section 4.4.3, page 115.

Unambiguous: *Thracia meridionalis* (1→0), Clade N (1→0).

ACCTRAN: Anomalodesmata (0→1), Parilimyidae (1→0), Septibranchia (1→2).

DELTRAN: Clade E (0→1), *Euciroa pacifica* + *Verticordia triangularis* + *Lyonsiella formosa* + *Poromya granulata* + *Cardiomya cleryana* (1→2), *Pholadomya candida* (0→1).

41. Connection between the distal tips of the left and right inner demibranchs, posterior to the visceral mass: ciliary (0); cuticular (1); tecidual (2). CI=0.5; RI=0.6; section 4.4.3, page 115.

Unambiguous: Archiheterodonta (2→0), *Verticordia triangularis* (2→0), Clade K (2→0).

ACCTRAN: Cleidothaeridae (0→1).

DELTRAN: *Cleidothaerus maxwelli* (0→1).

42. Interlamelar septa: absent (0); present (1). CI=1; RI=1; section 4.4.3, page 115.

ACCTRAN: Septibranchia (1→0).

DELTRAN: *Euciroa pacifica* + *Verticordia triangularis* + *Lyonsiella formosa* + *Poromya granulata* + *Cardiomya cleryana* (1→0).

43. Insertion of the ventral tips of the inner demibranch in the proximal oral groove: absent (0); present, involving fusion (1); present, not involving fusion (2). CI=0.66; RI=0; section 4.4.5, page 117.

Unambiguous: *Lyonsia norwegica* (2→1).

ACCTRAN: Heterodonta (0→2), Archiheterodonta (2→0).

DELTRAN: Anomalodesmata (0→2), Tellinoidea (0→2).

LABIAL PALPS

44. Morphology of labial palps: triangular flaps (0); reduced (1). CI=0.5; RI=0.83; section 4.4.4, page 117.

Unambiguous: Parilimyidae (0→1), *Euciroa pacifica* + *Verticordia triangularis* + *Lyonsiella formosa* + *Poromya granulata* + *Cardiomya cleryana* (0→1).

45. Sorting ridges on the oralward surface of the labial palps: absent (0); present (1). CI=0.5; RI=0.83; section 4.4.4, page 117.

Unambiguous: Septibranchia (1→0), *Parilimya* sp1 (1→0).

46. Position of labial palps: adjacent to the mouth (0); separated from the mouth by a long proximal oral groove (1). CI=0.5; RI=0.75; section 4.4.4, page 117.

ACCTRAN: Pandoridae (0→1), Palaeoheterodonta (0→1).

DELTRAN: Pandoridae (0→1), Palaeoheterodonta (0→1).

FOOT AND STATOCYSTS

47. Byssal apparatus in adults: absent or represented by vestigial ducts and a tiny groove (0); present, with a groove extending along the sole of the foot and an associated gland in the heel of the foot (1). CI=0.2; RI=0.75; section 4.5.1, page 118.

Unambiguous: Clavagelloidea (1→0), Clade K (1→0), *Euciroa pacifica* (1→0).

ACCTRAN: Heterodonta (0→1), Tellinoidea (1→0).

DELTRAN: Anomalodesmata (0→1), Archiheterodonta (0→1).

48. Opisthopodium absent (0); present (1). CI=0.33; RI=0.33; section 4.5.2, page 118.

Unambiguous: *Pholadomya candida* (0→1), *Periploma compressum* + *Pendaloma micans* + *Offadesma angasi* (0→1), *Asthenothaerus maxwelli* (0→1).

49. Position of insertion of the posterior pedal retractor muscle in the shell: dorsal or anterodorsal to the posterior adductor muscle (0); in the middle of the adductor (among the fibres of the posterior adductor muscle) (1); ventral to the posterir adductor muscle (2). CI=0.66; RI=0.66; section 4.5.3, page 118.

Unambiguous: Pandoridae (0→2), *Hunkydora novozelandica* (0→1).

ACCTRAN: *Myadora brevis* + *Myochama anomioides* (0→1).

DELTRAN: *Myadora brevis* (0→1).

50. Granules in each statocyst (statolith or statoconia): only one statolith (0); several statoconia (1). CI=0.33; RI=0.71; section 4.5.4, page 119.

Unambiguous: Clade E (0→1), *Laternula truncata* (1→0).

ACCTRAN: *Euciroa pacifica* + *Verticordia triangularis* + *Lyonsiella formosa* + *Poromya granulata* + *Cardiomya cleryana* (1→0).

DELTRAN: *Cardiomya cleryana* (1→0).

DIGESTIVE TRACT

51. Lateral grooves in the oesophagus: absent (0); present (1). CI=0.5; RI=0.75; section 4.6.1, page 120.

Unambiguous: Pholadomyoidea (1→0), Septibranchia (1→0).

52. Isolated duct from the digestive diverticula openning on the left side of the posterior floor of the stomach: absent (0); present (1). CI=0.2; RI=0.2; section 4.6.2, page 121.

Unambiguous: Clade K (0→1), *Trigonothracia jinxingae* (1→0), *Periploma compressum* + *Pendaloma micans* + *Offadesma angasi* (1→0), Clade N (1→0).

ACCTRAN: Pandoridae (0→1).

DELTRAN: *Pandora inaequivalvis* (0→1).

53. Posterior portion of the stomach expanded into a muscular sac: absent (0); present (1). CI=0.5; RI=0.8; section 4.6.2, page 121.

Unambiguous: Parilimyidae (0→1), *Euciroa pacifica* + *Verticordia triangularis* + *Lyonsiella formosa* + *Poromya granulata* + *Cardiomya cleryana* (0→1).

54. Fusion of style sac and midgut: present along the entire length of the style sac (0); style sac joined to midgut only at their opening on the floor of the stomach (1). CI=0.5; RI=0; section 4.6.2, page 121.

Unambiguous: *Poromya granulata* (0→1), *Cardiomya cleryana* (0→1).

55. Path of the descending intestine: runs postero-ventrally (0); curves anteriorly (1). CI=0.16; RI=0.58; section 4.6.3, page 124.

Unambiguous: Pandoridae (0→1), *Lyonsia norwegica* + Laternulidae (0→1), Clade K (0→1), *Trigonothracia jinxingae* (1→0), *Cochlodesma praetenue* (1→0), Archiheterodonta (0→1).

56. Passage of rectum with respect to the heart: rectum passes through the heart (0); rectum passes above the heart (1); rectum passes below the heart (2). CI=0.28; RI=0; section 4.6.3, page 124.

Unambiguous: *Pandora inaequivalvis* (0→1), *Pandora gouldiana* (0→1), *Pholadomya candida* (0→2), *Bentholyonsia teramachii* (0→2), *Euciroa pacifica* (0→2), *Cardiomya cleryana* (0→2).

ACCTRAN: Cleidothaeridae (0→1).

DELTRAN: *Cleidothaerus maxwelli* (0→1).

KIDNEYS AND GONADS

57. Kidneys extending laterally into the mantle: absent (0); present (1). CI=0.5; RI=0.66.

Unambiguous: *Euciroa pacifica* + *Verticordia triangularis* + *Lyonsiella formosa* + *Poromya granulata* + *Cardiomya cleryana* (0→1), *Euciroa pacifica* (1→0).

58. Reproductive mode: simultaneous hermaphrodite (0); dioecious (1). CI=0.25; RI=0.4; section 4.7, page 124.

Unambiguous: Anomalodesmata (1→0), *Clavagella australis* (0→1), *Bentholyonsia teramachii* (0→1), *Cardiomya cleryana* (0→1).

59. Thick capsule encasing each ovocite individually: absent (0); present (1). CI=0.33; RI=0.5; section 4.7, page 124.

Unambiguous: Anomalodesmata (0→1), *Bentholyonsia teramachii* (1→0), *Trigonothracia jinxingae* (1→0).